Edge effects in a forest mosaic: implications for oak regeneration in the Highlands of Chiapas, Mexico.

by

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A thesis submitted to the **University of Edinburgh** for the degree of

Doctor of Philosophy

2003

Declaration

I hereby declare that this thesis is composed of work carried out by myself unless otherwise acknowledged and that this thesis is of my own composition. The research was carried out in the period of March 2000 to September 2002. This thesis has not in whole or in part been previously submitted for any other degree or professional qualification.

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Acknowledgements

I would like to thank to my supervisors Adrian Newton, Colin Legg, Robert Manson and Mario González-Espinosa for their guidance on the research design, logistics of fieldwork, and the production of this dissertation. I especially appreciate the time that Adrian Newton and Robert Manson took to visit to the field site. I also wish to thank Duncan Golicher, Pedro Quintana-Ascencio and Colin Legg for providing assistance in the statistical analysis. Thanks to Neptalí Ramírez-Marcial, Susana Ochoa-Gaona, Bruce Haines and Mike Steele who offered relevant information and valuable comments during the research.

I am extremely grateful to the many people who helped at different stages with the fieldwork, including: Alfonso Luna-Gómez, Javier Bautista-Bolóm, Juan C. Bautista-Bolóm, Pedro Girón-Hernández, Maricela García-Bautista, Felipe Barragan-Torres, Henry E. Castañeda-Ocaña, Enrique Ocaña and José A. Montero-Solano. Miguel Martínez-Icó deserves a special mention for his invaluable assistance and enthusiasm on several field trips. I also wish to thank to Mario Guillén who provided me with the equipment that was necessary for the fieldwork. I am especially indebted to Consuelo Lorenzo-Monterrubio who kindly allowed me to use her live traps for small mammals and gave me access to the rodent collections. My thanks also to Oscar Retana who offered professional support in rodent manipulation and identification. I'm most grateful to Yolanda Barrera-López who helped to capture data and to tag thousands of acorns.

Many thanks to the owners of the study plots in Rancho Merced Bazom who provided access to the sites: Nicolas Martínez, Pedro Pérez-Martínez, Manuel Díaz-López, Pedro Martínez-Alvarez, Miguel Pérez-Martínez and Nicolas Pérez-Ton. I am grateful to the staff of SEMARNAT (Region Altos) who transferred the seedlings from the nursery to the field sites.

I am also grateful to Diego M. Díaz-Bonifaz for his assistance with map production, Hermilo Cruz-García, Mario Zuñiga-Trejo and Maria E. Martínez-Pérez for

maintaining an efficient library service at ECOSUR. My thanks to other staff in ECOSUR including Mario Ishiki-Ishihara, Abraham Mena-Farrera, Carla Gasca-Suárez who were always very helpful. Thanks to Efraín Ascencio-Cedillo for helping me with the pictures.

Particular thanks to Graham French, Cécile Bâcles, Simoneta Negrete-Yankelevich, Barbra Harvie and Tanya Ogilvy for stimulating conversations and advice during the writing up stage. Recognition is extended to the administrative and technical staff in the Institute of Atmospheric and Environmental Science at the University of Edinburgh, including Graham Walker and Connie Fox.

El Colegio de la Frontera Sur (ECOSUR) provided nursery and part of the fieldwork facilities. I also visited the Instituto de Ecología A.C. Xalapa, Mexico and the World Conservation Monitoring Centre, Cambridge, over the course of the research. The British Council provided a scholarship for the first year of this research (Chevening programme Mex-2900177) and the "Consejo Nacional de Ciencia y Tecnología" (CONACYT) then funded the following three years (scholarship 131197). CONACYT also covered part of the research expenses. Financial support to pay the rent for the study plots was provided by the European Commission under the INCO-DC programme (framework 4) as part of the SUCRE project (ERBIC-18 CT 97-0146) and the BIOCORES project (PL ICA4-2000-10029).

Dedication

To my parents

Yolanda Barrera López

and

Roberto López Alexandre

La culminación de esta tésis fue gracias al constante
apoyo y estímulo de mi familia: **Y**olanda, **R**oberto, **L**orena y **R**oberto.
Mis amigos: **O**lga, **E**fraín, **J**osé **A**ntonio, **G**abriel y **T**arin
y a la tolerancia de mi compañero de siempre, de vida… **J**osé **A**ntonio.

ABSTRACT

Forest edges created by scattered-patch clear-cutting have become a common landscape feature in tropical montane forests, including pine-oak and evergreen cloud forests. Forest-edge-pasture gradients were characterised with respect to changes in vegetation structure and ecological function in the Highlands of Chiapas, Mexico. In this study two edge types were recognised by assessing vegetation structure and floristic composition along a gradient from adjacent clearings into the forest interior. The influence of edge type (either "hard" or "soft") was investigated with respect to acorn production, predation, dispersal and germination, seedling establishment and abundance of small mammals during two consecutive years.

There was no significant difference between the forest interior and the edge in plant density and basal area. Floristic richness and composition did not vary with depth-of-edge influence. Edge type influenced the relationship between probability of acorn removal by small mammals and distance from the edge in both mast fruiting and non-mast fruiting years. Movements of metal-tagged acorns supported the hypothesis that soft edges are permeable to acorn predators and/or dispersers, and that rodents move acorns up to 15 m into the grasslands in soft edges. In hard edges, acorn dispersal and removal was greater within the forest. *Peromyscus* spp. were the main acorn predators and/or dispersers of acorns. The intensity and rate of acorn removal varied with the year, demonstrating that in mast-fruiting years some seeds may escape predation by animals, according to the predator satiation hypothesis. Grasslands presented fewer insect damaged acorns and higher seedling emergence than the edge and the forest, emphasising the importance of acorn dispersal. Seedling survival and growth were higher for 12 m into grassland from the soft edges, suggesting that the probability of oak expansion into the grassland increases when the grasslands have been abandoned and have a scattered cover of shrubs.

The results indicate that edge structure alters edge function (edge permeability), which determines the probabilities of tree invasion into old-fields. These findings have implications for the conservation of montane forest in Mexico where scattered-

patch clear-cutting is widespread. Recommendations are made for different restoration practices to accelerate tree colonisation into the grasslands across hard and soft edges.

Contents

CHAPTER 1: General introduction and context of research

INTRODUCTION

The mountains of tropical Latin America are one of the world's great centres of biodiversity, and have recently been identified as a global conservation priority (Aldrich *et al.* 1997; Myers *et al.* 2000). The Neotropics are home to more than 90,000 species of flowering plants, and of these, 45,000 are found in montane forests. These Neotropical mountains are also characterised by an impressive diversity of fauna, environment, climate and people (Churchill *et al.* 1995; Bruijnzeel 2003). Montane ecosystems offer a tremendous array of biological resources with great economic potential for the region and the world, being the centre of domestication of wheat, corn, rice and potato (Churchill *et al.* 1995). Although tree diversity in montane forests is lower than in lowland tropical forests, a major contribution to total species richness is made by shrubs, epiphytes, herbs, fungi, lichens, liverworts and mosses (Churchill *et al.* 1995; Mueller & Halling 1995).

Floristically montane cloud forests are distinctive compared to both lowland and lower montane rain forests (Webster 1995; Ramírez-Marcial *et al.* 2001), containing genera of both Northern and tropical elements. Northern genera such as *Quercus, Liquidambar, Fagus, Illicium* and *Magnolia* reach no further south than Panama or Colombia. The Highlands of central and eastern Mexico are the major centre of diversity for the genus *Quercus* (oaks) (Nixon 1993). According to recent estimates there are 202 species of *Quercus* in the New World. Mexico has the greatest number of species with 135-140 species (46% belong to the subgenus *Leucobalanus*, 51% to *Erithrobalanus* and 3% to *Protobalanus*), of which 86 are endemic (Nixon 1993; Zavala-Chávez 1998). Oak species compose the canopy of many forest associations in the mountains of tropical Mexico and Central America and occur mostly as evergreen and semi-evergreen trees, as the sole dominant, or often in association with pine (Nixon 1993).

Humans began altering Neotropical montane forests thousands of years ago, when mountain landscapes were colonised by the original settlers (Challenger 1998), but recently, increasing human population pressure has threatened the conservation of these forests (Churchill *et al.* 1995). Previous research in the Highlands of Chiapas, as in other neotropical montane forests, has documented increasing forest fragmentation that results in increased numbers of small and isolated forest patches bordered by open habitats (Ochoa-Gaona & González-Espinosa 2000; Ochoa-Gaona 2001; Ochoa-Gaona *et al.* 2003). The extent of such changes underlines the need for a better understanding of how contrasting adjacent habitats affect ecological processes. This study represents the first attempt in these montane forests to test experimentally how different anthropogenic edge types affect ecological processes both within the forest and in the adjacent open habitats.

Most of the previous studies about edge effects have been conducted in well-preserved lowland tropical forest fragments and have evaluated the effects of edges on microclimatic and vegetation patterns within the forest community (Williams-Linera 1990a; Williams-Linera 1990b; Malcolm 1994; Kapos *et al.* 1997; Turton & Freiburger 1997; Laurance 1997; Fox *et al.* 1997; Benitez-Malvido 1998; Laurance *et al.* 1998; Didham & Lawton 1999; Sizer & Tanner 1999; Gascon *et al.* 2000; Laurance & Williamson 2001). Several studies have also been undertaken focusing on edge effects on vegetation and microclimate in temperate forests (Wales 1972; Ranney *et al.* 1981; Chen *et al.* 1992; Matlack 1994; Chen *et al.* 1995; Goldblum & Beatty 1999; Hansson 2000ab; Gehlhausen *et al.* 2000; Euskirchen *et al.* 2001; York *et al.* 2003; Chen *et al.* 1992) but there are fewer studies in neotropical montane forests (Williams-Linera 1993; Jose *et al.* 1996; Oosterhoorn & Kappelle 2000). Other studies have tested edge effects on plant regeneration processes such as seed and seedling predation and seedling establishment (Burkey 1993; Holl & Lulow 1997; Restrepo & Vargas 1999; Bonfil & Soberon 1999; Diaz *et al.* 1999; Meiners *et al.* 2002; Jones *et al.* 2003; Restrepo & Vargas 1999). Recently more studies have explored the factors that modulate edge effects on plant regeneration (Ostfeld *et al.* 1997; Manson & Stiles 1998; Manson *et al.* 1998; Manson *et al.* 1999; Restrepo *et al.* 1999; Mesquita *et al.* 1999; Honnay *et al.* 2002; Kupfer & Runkle 2003). Very

few studies have classified functional edge types and tested mechanistic hypotheses (Fenske-Crawford & Niemi 1997; Fleming & Giuliano 1998; Cadenasso & Pickett 2000; Cadenasso & Pickett 2001; Honnay *et al.* 2002; Kollmann & Buschor 2002). None to my knowledge has tested mechanistic hypotheses in different edge types on plant regeneration processes both within the forest and within the adjacent open areas.

In the Highlands of Chiapas, the establishment of woody vegetation by natural dispersal into abandoned grasslands or shrub fallow lands is one potential mechanism for the recovery of the degraded forest landscape. The occasional reduction of the grazing stocking rate or the temporal abandonment of agricultural clearings may promote rapid establishment and growth of some woody species. These species may suppress dominant grasses and influence the microclimate and soil fertility, they may also attract animal seed dispersers that in turn may facilitate the regeneration of other intermediate or late-successional shrubs or trees (Wunderle 1997). However, most of the research into seed colonisation on open areas relies on field surveys of seedlings and saplings of woody vegetation (González-Espinosa *et al.* 1991; Montes-Avelar 2001), rather than experimental analyses. The observed patterns of woody colonisation may be the result of failure of seeds to arrive and/or the lack of suitable conditions for seedling establishment. Proximity to the forest edge is critical also for species that are dispersed from the forest by animals that move short distances into contiguous old-fields (Kollmann & Schill 1996; Herlin & Fry 2000). How the different edge types enhance or retard the dispersal of propagules from the forest to adjoining old-fields is not known. How the edge affects the movement behaviour of seed dispersers is a key question to understand the patterns of woody colonisation into open areas and the potential recovery of the abandoned fields.

Animal-mediated processes can be severely affected by habitat fragmentation as most animals are highly sensitive to habitat loss (Asquith *et al.* 1997; Bayne & Hobson 1998; Lidicker 1999; Harrington *et al.* 2001). Within the tropical montane forests, several oak species contribute to a wide range of biological resources and are key-species for insects, mammal and bird species (Quintana-Ascencio *et al.* 1992;

González-Espinosa *et al.* 1995). It has been documented that small mammal populations rely on acorns as an important food source (Wolff 1996) and acorns rely on small mammals as potential seed dispersers (Miyaki & Kikuzawa 1988). The fragmented oak forests of Chiapas therefore provide an outstanding opportunity to study how the presence of the edge and different adjacent vegetation may affect this plant-animal interaction along the forest-edge-grassland gradient.

The dispersal phase is one of the most critical in plant life histories (Howe & Smallwood 1982) and is crucial to determine genetic structure and range expansion rates. The effectiveness of seed dispersal (i.e. the probability of successful recruitment from seed during some period) is dependent on the following factors: seed production, vector of seed transport, timing of seed release or removal, distance of dispersal and ultimate fate of dispersed seeds (predation, germination and seedling establishment). Seldom have these factors been examined in detail in one study (Schupp 1990; Van der Valk 1992). Most of the research that links seed dispersal or removal with spatial processes is related to the test of the Janzen-Connell hypothesis (Howe *et al.* 1985; Burkey 1994; LoGiudice & Ostfeld 2002). There is therefore a lack of research that has investigated all these processes with a spatially explicit approach other than distance to the parent tree (Nathan & Muller-Landau 2000).

The main objective of this study is to evaluate the effects of two edge types at small spatial scales within a highly dynamic forest mosaic. A spatial approach was used to study key oak regeneration processes along the forest-edge-grassland gradient. Through this general introduction, firstly, I present a description of the land use patterns in the Highlands of Chiapas and I describe briefly which are the present threats to montane forests that highlight the need to study edge effects. I then present the context of research that includes a review of the terms and theories relating to edge effects. Finally, the structure of the thesis is described, with general objective and hypothesis, the research structure and key questions for each chapter of this dissertation.

STUDY AREA

Huistan: a forest mosaic in the Highlands of Chiapas, Mexico

The central mountainous region of Chiapas sustains sizeable indigenous human populations. For at least a thousand years the Tzotzil and Tzeltal-speaking Maya have lived in the valleys of this plateau. The economy of the Highlands is based on the growing of corn, beans, and squash, using the age-old methods of slash-and-burn agriculture called "Milpa" (Nigh 1975; Collier 1975). The high biological and cultural diversity in this region have attracted the attention of researchers who have documented historic, social, cultural, political, economical and biological processes (Miranda 1952; Nigh 1975; Collier 1975; Whitmeyer 1997; De Jong *et al.* 1999; Konstant *et al.* 1999). In the Highlands, the Tzotziles and Tzeltales are organised into communities, each with their own social and cultural identity and boundaries that generally coincide with the modern municipalities.

Huistan (at an elevation of 1600-2700 m) is one of the 18 municipalities that comprise the Highlands of Chiapas. It is one of the most populated areas with 17669 inhabitants (in 319 km^2) recorded in the census of 1990, and 85% of the economically active population is devoted to agricultural activities. About 61% of the owners have small plots (< 5 ha in total) dispersed in different topographic locations. (Ochoa-Gaona 2001). In Huistan, as in most of the Highlands, the traditional slash and burn agriculture is the main element that drives the forest fragmentation process (Ochoa-Gaona 2001). Agriculture predominates since the soils show a medium to high content of bases with loamy horizons that are intersected by watercourses that make them more suitable for agriculture than other soils in the region (Ochoa-Gaona & González-Espinosa 2000). Since pre-Columbian times the region has had a basic pattern of self-sufficiency in production and has been isolated from the commercial world due to the political disorganisation and the low ecological potential compared to the lowlands (Nigh 1975).

The Spanish conquest radically altered the environment of the region. Expansion of newly introduced cattle ranching rapidly reduced the amount of forested land. Spaniards in the colonial capital of Ciudad Real (now San Cristobal de Las Casas) demanded food (grains, fruits and vegetables) from the nearby Indian communities. Agricultural practice in Huistan is unique in the Highlands, as it has been influenced by European farming techniques. Huistecos used the oxen for ploughing and they were the most important providers of wheat, the grain most precious to the Spaniards, since the colonial period.

Modern Mayan agricultural practices in Huistan, as in the rest of the Highlands, are the same as they were three thousand years ago, which is why they are considered a pre-conquest Mayan technique that survives from the ancient Mesoamerican pattern (Nigh 1975). The agricultural cycle begins with land preparation for seeding. The land is burned during March and April (end of dry season) to destroy roots and seeds of undesirable weeds. Crops are seeded when rain is sure (May-June) to stimulate germination before seeds are predated. Weeding is necessary, sometimes twice, during July to August. During the beginning of the dry season (October-November) when leaves, stalk and husk are dry, the corn and the beans are harvested (Nigh 1975). Burning and cultivation inevitably reduce the total biomass of the crops, and lead to loss of mineral nutrients (Fig.1.1). By abandoning the fields farmers allow the natural successional process to supply the energy and materials needed to restore fertility after cropping.

In Huistan, as the agricultural activity depends on the manual labour of the farmer and his family, the maximum area that can be cultivated in any year is about four hectares (Ochoa-Gaona & González-Espinosa 2000). Independent of the amount of land that each farmer owns, the common pattern of land use is to cultivate various small Milpas under different environmental conditions. Therefore, if a naturally induced disaster occurs at one location, the entire crop will not be lost. If farmers have enough land available, they first eliminate forest vegetation in the valleys where soils are deeper usually close to water sources. When a family needs to cultivate more land to support their basic needs or when the fertility of the soils is depleted,

new Milpa fields are expanded onto the hillsides. When the initial land selection criteria of the fertile soils and sufficient water supply can no longer be met, the dominant criterion becomes the availability of land, independent of its agricultural potential (see review in Ochoa-Gaona 2001).

Fig 1.1 Alfonso Luna-Gomez (field technician) in a typical Milpa after slash and burn in Rancho Merced Bazom, Huistan. The stump shown is from *Magnolia sharpii*.

This production system maintains a sequence of Milpa-fallow-Milpa, resulting in a landscape mosaic that includes small clearings, agricultural lands (0.5 to 2 ha) such as grasslands and shrublands, and secondary forest showing a varying dominance by either pines or oaks (González-Espinosa *et al.* 1991). The small remnants of original vegetation currently occur only where topography makes agriculture difficult and include associations of evergreen cloud forest, oak forest and pine-oak forest (Breedlove 1981; González-Espinosa *et al.* 1995).

The nature of forest succession after agricultural use is related to several factors such as altitude, soil fertility conditions, remnant seeds or roots in the soil (resprouting), spatial position of the clearing relative to the seed sources, abundance of seed dispersers and fallow management (Kammesheidt 1999; Ochoa-Gaona & González-

Espinosa 2000; Montes-Avelar 2001; Chinea 2002). A brief description of the successional seres obtained from a study by González-Espinosa *et al.* (1991) in Huistan is presented below:

1. Recently abandoned Milpa: Fallow 3-4 years after the last Milpa cultivation. Usually grazed by sheep. Only one prostrate vegetation layer and only about 49% of the ground is covered with herbaceous species (for example: *Dyssodia papposa, Setaria geniculata, Trifolium amabile*). About 10% of the area is covered by leaf litter and 40% is bare ground.
2. Grasslands: Grazed by sheep (this seral stage may remain stable thorough time if moderately grazed) and covered (98% of the area) with only one herbaceous layer. Dominant grasses are *Sporobolus indicus, Paspalum jaliscanum* and *Vulpia bromoides*. Some seedlings of the shrub *Baccharis vaccinioides* may occur in these seres.
3. Shrublands: Vegetation with at least three vegetation layers. Prostrate vegetation layer only covers about 5% of the ground, 35% is covered by litter and 4% by bare ground. Shrub cover (60% of the area) is dominated by *Baccharis vaccinioides, Rubus* spp. *Stevia ovata* and *Stevia serrata*. Vigorous saplings and regeneration of pines and oaks are present in these seres.
4. Early-successional forest: The most frequent mean age of pines 20-25 years. Dominant trees form a canopy of 80-90% cover at a height of 10-15 m. A few small epiphytes occur on the largest branches. Saplings of pines and oaks (<15 cm DBH) are highly abundant (7300 individuals per ha). Fuelwood and/or small poles are occasionally collected.
5. Mid-successional forest: Mean age of the oldest pines is 40-45 years. Canopy cover is 70-80% at a height of 20-25 m. Bromeliads, orchids, and epiphytic ferns cover most of the large branches. Oaks and pines are dominant in the canopy (*Q. laurina, Q. rugosa, Q. crassifolia, Pinus tecunumanii, P. pseudostrobus* var. *pseudostrobus* and *P. montezumae*) and the understorey layer (10-12 m high) is dominated by *Rapanea jurguensenii, Symplocos limoncillo, Oreopanax xalapensis, Fuchsia* spp. and *Litsea glaucescens*. The herbaceous layer is dominated by *Zeugites americana* var. *mexicana, Adiantum andicola,* and *Hydrocotyle umbellata.*

6. Mature forest: The oldest pines have a mean age of 80-100 years. There is an open canopy at 35-45 m dominated by *Q. laurina* and *Q. crassifolia*, and a more continuous understorey tree layer at 8-12 m dominated by *Rapanea juerguensenii, Oreopanax xalapensis, Ternstroemia pringlei, Cleyera theaeoides* and *Rhamnus* sp. There is pine regeneration under the canopy. A heavy cover by diverse epiphytes, high number of herbaceous ferns, vines and lianas are characteristic of this forest. The shrub layer included *Fuchsia* spp., *Litsea glaucescens, Xilosma chiapensis* and *Senecio* spp. The herbaceous layer is dominated by *Zeugites americana* var. *mexicana, Hydrocotyle umbellata, Adiantum andicola, Asplenium monanthes* and *Polypodium plesiosorum.*

The replacement of a herbaceous community by a three-layered vegetation may occur in 15-20 years and the development of a floristic composition typical of an old-growth or mature forest may occur in 60-80 years (González-Espinosa *et al.* 1991). Faster secondary succession may occur when more fertile abandoned cornfields revert directly to gradual shrub growth if grazing is suppressed and land fertility is not exhausted by cultivation (Collier 1975; Montes-Avelar 2001). Resprouting from stumps of tree species such as *Quercus, Alnus, Liquidambar, Prunus* and *Arbutus,* and nearby availability of seeds of tree species may accelerate the secondary succession process after Milpa abandonment (Ramírez-Marcial *et al.* 1992).

Indigenous people regularly collect traditional forest products from both old-growth forests as well as early- and mid-successional forests following Milpa abandonment. Hunters shoot deer, squirrels and a variety of other animals, which are becoming scarcer. Indigenous people also gather wild berries, bromeliads, mushrooms and some herbs and medicinal plants are cultivated near homes. Pine trees are cut for timber production and for home construction, therefore pines are usually left to grow to attain conventional logging sizes (>30 cm DBH and > 20 m high). This specific use allows pines to have several reproductive events and to colonise forest edges and recently abandoned crops or grasslands. Generally, logged pine forests are later used for extensive grazing of cattle or sheep whereas pine-oak and oak forests are continuously logged for timber, fuelwood and charcoal production or are converted

into Milpa or pasture (González-Espinosa *et al.* 1991; Alemán-Santillán 1997; De Jong *et al.* 1999).

Local communities depend strongly on oaks for fuelwood and for the production of charcoal to supply their energy needs (and occasionally to be sold in local markets). Oak species may reach considerable heights if allowed to develop to adult stages (>30 m), but they are frequently subjected to selective logging. Resprouting shoots of oaks can be further used as fuelwood, but this does not allow them to grow to their original condition (González-Espinosa *et al.* 1995). This pattern of use of oaks may also limit their mast seeding events due to the trade-off between growth and reproduction.

As a consequence of these patterns of forest use, mixed pine-oak canopies may be replaced by mostly pine-dominated canopies (Galindo-Jaimes *et al.* 2002). In Huistan a major landscape transformation between 1974 and 1996 involved a change from pine-oak forest to pine forest and secondary vegetation (Ochoa-Gaona & González-Espinosa 2000). Once pines are removed from the canopy, juveniles of either pines or oaks may subsequently dominate the canopy, however this pattern is not very frequent in Huistan as only 4% of pine forest reconverted to pine-oak forest between 1974 and 1996 (Ochoa-Gaona & González-Espinosa 2000).

The relative importance of natural and anthropogenic disturbance and environmental conditions affecting successional pathways and a climax forest in Huistan as in the rest of the Highlands is not well understood. The prevention of a steady-state or climax forest from being achieved may be due to natural and anthropogenic disturbance. Observations in relatively preserved forest or mature forest suggest that occasional but severe windstorms may maintain an open canopy (González-Espinosa *et al.* 1991). This pattern is similar to that reported for other forested mountain area in Mexico where wind affected 1% of the forest area every year by creating canopy gaps (Arriaga 1987). Periodic surface fires in forest edges adjacent to clearings in the study area may occur but they are associated with the Milpa cultvation when fire is

not controlled by the farmer. However, fire has not been considered as a relatively important natural disturbance factor driving successional pathways.

The anthropogenic disturbance regime since pre-Columbian times has been even less predictable and their effects are more complex due to the different type and intensity of use of the seral stages after the Milpa cultivation. Previous research has documented that pines or oaks tend to dominate each other in the canopy of forest stands subjected to various degrees of disturbance, and numerous broad-leaved species in the understorey are dependant on an oak-dominated canopy to regenerate (González-Espinosa *et al.* 1995; Galindo-Jaimes *et al.* 2002). However, it has also been documented that in the most humid habitats such as the Evergreen Cloud Forest fragments there is a canopy (25-35 m) dominated by broadleaved species including *Persea, Stirax, Clethra, Chiranthodendron, Olmediella, Liquidambar, Cleyera* and occasional *Quercus acatenangensis* and *Q. laurina* (González-Espinosa *et al.* 1997; Ramírez-Marcial *et al.* 2001). Further research is needed to establish whether pine-oak and oak dominated forest represent temporal successional stages (or anthropogenic climax) towards a climax forest dominated by broad-leaved species in the canopy as has been documented in other less disturbed Mexican montane forests (Ramírez-Marcial *et al.* 2001).

Present threats to forest conservation and regeneration

Traditional shifting agriculture may be sustainable because it leads to secondary succession and the recovery of diversity and productivity of the mature forest. Rapid reforestation following agricultural decline has obscured much of the past land use and confirms the resilience of some tropical forests to intensive human disturbance (Attiwill 1994). However, as has occurred in many other tropical mountain regions, in the Highlands of Chiapas the human population has outstripped the capacity of farming within a stable traditional shifting system (Collier 1975; Pool-Novelo 1997). In response to population growth mainly between 1950 and 1990 (the population of the region tripled) and restricted access to additional lands, a shortening of the fallow period was recorded. As a result the amount of forest diminishes and fields must be

cleared before the regenerative process of succession has run its full course, thus a gradual shift occurs from tree fallow regime to a bush fallow system (Nigh 1975). If fallows are not long enough to restore soils to their productive capacity there is often a need for greater input (of fertilisers, herbicides, etc.) in order to maintain the clearing (Montagnini & Mendelsohn 1997). Additionally, fallow land is often grazed by sheep or cattle resulting in permanent grasslands that limit shrub or woody vegetation recruitment (Quintana-Ascencio *et al.* 1992; De Jong *et al.* 1999).

Ochoa-Gaona (2001) documented patterns of forest fragmentation and degradation in Huistan from 1974 to 1996. She found that deforestation occurred patchily and an indeterminate fragmentation pattern was recorded due to continuous successional changes, both progressive and regressive between Milpa fields and tree fallows, resulting in a forest mosaic. The total number of fragments (<10 ha) of dense forest increased by 8.9% per year in Huistan, and the distance between dense forest fragments increased and produced higher isolation between them. She documented that in 1974 a dense forest fragment occupied 50% of the municipality, whereas in 1996 it occupied only 0.4% of the area (Table 1.1). In the Highlands, as in Huistan, fragmentation patterns are not simple. Large fragments may present an irregular shape with a large length of edge due to linear openings within the core area. When these large forest fragments are transformed into smaller fragments or transformed into perturbed forest, the result is a landscape with small and more isolated fragments that have more regular shapes and less edge length (Ochoa-Gaona *et al.* 2003). For this reason, the total edge length of dense forest fragments between 1974 and 1996 decreased.

Considering the studied and observed patterns of recent fragmentation and changes in land use in Huistan, it is noticeable that the most common adjacent habitats within the forest mosaic are forest fragments with various levels of disturbance and crops, grasslands or shrublands (Fig. 1.2). It has been documented that smaller fragments of dense forest (1.5 ha or less) surrounded by open areas can be considered as disturbed because of the large border area (Ochoa-Gaona 2001).

Table 1.1 Fragmentation indices for Huistan municipality in 1974 and 1996. Modified from Ochoa-Gaona (2001). Secondary vegetation includes tree and shrub fallows. Open areas include grasslands, croplands, bare soil and settlements.

Index	Dense Forest		Disturbed forest		Secondary Vegetation		Open areas	
	1974	1996	1974	1996	1974	1996	1974	1996
Total area (ha)	17933	2282	2282	8152	9130	13368	3261	8804
Number of fragments	154	553	595	584	615	582	261	464
Mean fragment size (ha)	117	4	4	14	15	23	12	19
Total edge (km)	1211	510	608	1445	1298	1774	411	948
Total edge contrast (%)	44	30	40	47	56	62	80	78
Mean nearest neighbour distance (m)	82	115	184	114	153	109	670	277

However, there is no information available about whether the edge in this system contributes to the process of degradation, which may favour secondary species and negatively affect understorey species. The level of impact may depend on the level of matrix contrast resulting from these different edge types and on the adaptability of species to adjust to the relatively new conditions (Ochoa-Gaona & González-Espinosa 2000).

In addition to the increase of the agriculture frontier and permanent deforestation, there has been a degradation of forest structure and floristic composition. In recent years the extraction of forest products has changed from predominantly self-sufficient towards market-driven use in order to support farmers' incomes (Montoya-Gomez 1998; Ochoa-Gaona & González-Espinosa 2000). Mono-specific pine-dominated open canopies are enhanced due to their potential economical value and are replacing mixed or oak forest. The potential consequences include a decrease in the biodiversity associated with humid and shaded microenvironments characteristic of montane forest. Oak-dominated canopies present higher richness of broad-leaved species compared with mixed forests or pine-dominated canopies.

The pinelands include only 20-60% of the number of species of ferns, vines, lianas, shrubs, and understorey trees of those occurring in neighbouring stands with an oak-dominated canopy (González-Espinosa *et al.* 1995). Similarly, Ramírez-Marcial *et al.* (2001) documented that frequent anthropogenic disturbance in montane rain forest resulted in a dominance of *Pinus* species and a drastically decreased floristic richness, mostly comprising understorey tree species of Pantropical distribution.

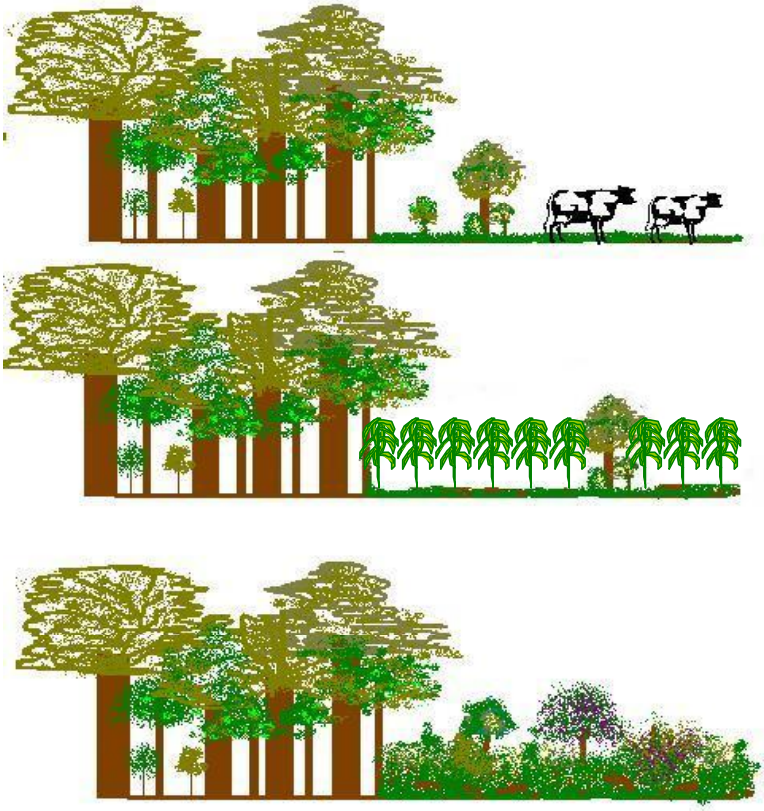

Fig. 1.2 Common non-forested habitats adjacent to the pine-oak forest. From top to bottom, permanent grassland, Milpa and abandoned clearing with scattered presence of shrubs.

CONTEXT OF RESEARCH

Basic concepts: Edges

Edge is the name given to the area or transition zone that separates habitat types and is perceived by some focal organism as being significantly different in quality (Lidicker 1999). Such boundaries are critical features in the understanding of habitat heterogeneity (Wiens 1995) and influence both the ecosystem structure and function through their roles as sites of exchange of energy, materials, and organisms between patches (Wiens *et al.* 1985). The term "patch" typically implies a discrete and internally homogeneous entity and "contrast" is the degree of difference between patches or between patch and matrix (Wiens 1995).

Other concepts such as ecotones and boundaries have been used in the literature as synonyms of edges, and there are not clear differences between the use of these terms. Sarlov-Herlin (2001) reviewed all of these terms and said that the ecotone concept has been associated with transition zones for broader scale studies, as in terrestrial-aquatic transitions, or even between continental scale biomes. In landscape research, the "boundary" concept is broadly used to imply a range of meanings, from an administrative border, to an analogue for "ecotone", however as presented recently in landscape ecology, boundaries are viewed as filters or semi-permeable membranes, which can regulate flows of materials, species and energy between patches in a landscape mosaic (Wiens *et al.* 1985; Sarlov-Herlin 2001; Laurence *et al.* 2001).

Edge definition and measurement depend on habitat definition for focal species and the spatial scale of the study (Murcia 1995; Sarlov-Herlin 2001). Therefore, habitat edges generate several restrictions (Lidicker 1999): a) the recognition of habitat edges will depend on the human observers, b) habitat edges separate two or more different habitat types and will be species-specific and possibly sex and age specific as well, and c) it will be difficult to measure the width and length of habitat edges, as various abiotic and biotic factors penetrate to different distances across an edge and it is therefore necessary to determine which ones are relevant to the focal organisms. Most studies that measure edge effects determine a "zero" meter mark but only a few indicate the criteria used to establish that point (Murcia 1995). It is very important to specify the precise placement of this mark with respect to tree trunks, canopy limits and the understorey stratum to make the study comparable with others. Some studies of vegetation responses to edge define the edge as the bases of bordering mature forest tree stems (Jose *et al.* 1996; Oosterhoorn & Kappelle 2000).

Edge classifications

The characteristics of the edge itself (thickness, sharpness, etc.) influence not only the movement within or across edges, but also the movement across edges and over adjacent patches in the landscape (Sarlov-Herlin 2001). Stamps *et al.* (1987)

considered the effects of edge permeability on movement behaviour and consequent demographic effects. Duelli *et al.* (1990) suggested that permeability is an important feature in edges and proposed six edge types based on the "hardness" for the focal organism. Edge types produced by human use have been described by Ranney *et al.* (1981), who identified three edge types (cantilevered, canopy dripline and advancing) based on where an edge was created and where it has been maintained. Sarlov-Herlin (2001) classified edges based on the shape (curvilinear and straight) and resolution (hard and soft) and all their possible combinations. Different functional edge types have been compared in few experimental studies and have resulted in the following *a priori* edge type classifications: 1) thinned vs. intact (Cadenasso & Pickett 2000; Cadenasso & Pickett 2001; Kollmann & Buschor 2002), 2) natural vs. anthropogenic (Song & Hannon 1999), 3) hard vs. soft edges (Fenske-Crawford & Niemi 1997) and 4) border-edge cuts vs. uncut edges (Fleming & Giuliano 1998).

Edge effects

The term "edge effect" was first used in 1933 by Leopold, a wildlife ecologist, to explain the particular richness of game species at edges between two habitats (Sarlov-Herlin 2001). Later the concept included the negative impacts of edges within large and well-preserved forest fragments (Fox *et al.* 1997; Benitez-Malvido 1998; Gascon *et al.* 2000). As applied to tropical countries, studies regarding reserve design were the first to address the issue of edges in the planning of protected areas (Laurance 1991). Nowadays, the concept comprises a wide range of processes occurring at edges, as mutual influences and ecological flows resulting in changes of species and structure (Lidicker 1999; Fagan *et al.* 1999; Cadenasso & Pickett 2000; Cadenasso & Pickett 2001; Laurence *et al.* 2001).

Edge effects may be defined by changes in any response variable, which occur at the transition between adjoining habitats (Lidicker 1999). The current use in the literature of the edge-effect concept summarises a diverse group of responses. Edges may have positive and negative consequences for focal organisms and it is important

to know whether or not they produce emergent response properties (Fig. 1.3). Lidicker (1999) proposed two general edge effects depending on these emergent properties: the matrix effect and the ecotone effect. The matrix effect is an abrupt change in some response variable as the edge is crossed and will reflect the fact that the response of organisms at an edge can be explained strictly by the organism's behaviour when separate in those habitat types (away from the edge). This type of boundary is defined as a "hard edge" by Duelli *et al.* (1990) (Fig. 1.3). The ecotonal effect is characterised by the presence of emergent properties (negative, positive or mutual influence), therefore the response of that organism at the edge cannot be explained by its behaviour in the two habitat types in isolation (Lidicker & Peterson 1999). Emergent properties could produce an increased or decreased response near the edge (Fig. 1.3).

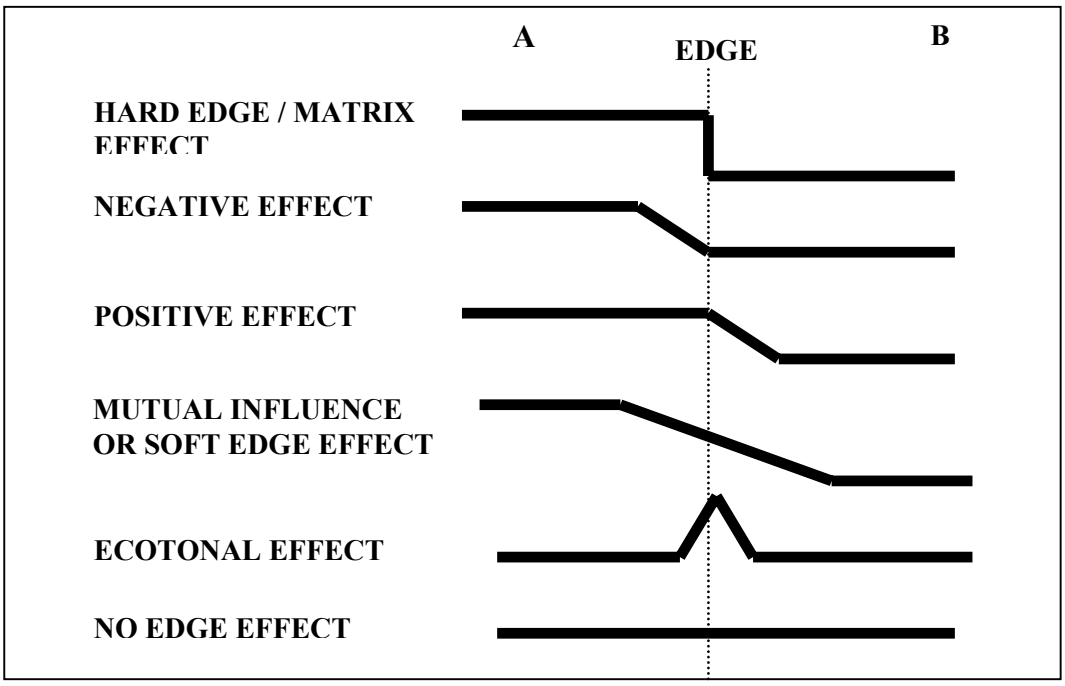

Fig. 1.3 Representations of some potential edge effects for any response variable. A and B are two juxtaposed habitat types. See text for explanation. Modified from Duelli *et al.* (1990).

Edge effects on species interactions

The effect of habitat fragmentation on species interactions has been extensively tested mainly on nest predation by mammals and other birds (see review by

McCollin 1998). Edges are believed to be detrimental to some bird species due to reduced reproductive success associated with increased rates of nest parasitism and predation. However, investigation of the effects of distance from the edge on the nesting success of birds has shown mixed results. Not all studies have documented edge effects and the general patterns seem to vary according to region, ecosystem, predator assemblage, forest size and type of adjoining habitat (Andren 1994; Murcia 1995; McCollin 1998; Brand & George 2000; Bergin *et al.* 2000; Hansson 2000a). It seems that an edge-related increase in nest predation is most commonly found inside small forest patches surrounded by farmland or highly fragmented landscapes and is rarely found or not detectable in forest mosaics or unfragmented landscapes (Donovan *et al.* 1997; McCollin 1998).

The edge effects on seed and seedling predation have been less studied than nest predation (see review in Chapter 3). There are no comparisons of these effects on forests mosaics or forest surrounded by disturbed or urban habitats. Small mammals are important seed predators and/or dispersers. The small mammals' type of habitat use (specialist or generalist) will have a great influence on the outcome of an edge seed-predator interaction (Lidicker 1999; Manson *et al.* 1999) and will determine the seed predator and/or disperser's ability to move across edges between adjacent patches of different quality (Rodriguez *et al.* 2001).

Edge effects on seed dispersal are caused by associated changes in vegetation structure near the edge (Kollmann & Buschor 2002), however most edge effect studies on regeneration processes do not include a precise description of the edge structure. There is substantial discrepancy among recent studies about the existence and intensity of edge effects on seed predation (Kollmann & Buschor 2002). Some of the lack of consistency in the results may be attributed to improper design (lack of true replication), lack of consistency in edge definition and methodology, lack of temporal replication and oversimplification of the perception of edge dynamics (Murcia 1995) and also to the temporal and spatial variability in the occurrence of different seed predators.

THESIS OUTLINE

General objective and hypothesis

The aim of this research is to investigate the effect of different anthropogenic edge types on key oak regeneration processes along the forest-edge-grassland gradients.

A general landscape theory is that as structural similarity increases between two adjacent habitats, the edge created becomes less abrupt and the edge effect less evident. This also may lead to the prediction that ecological flows (such as animal movements) across edges may be reduced as edge sharpness or abruptness increase. In this study, the general hypothesis was based on this theory and in the particular differences between hard and soft edges. It is expected that hard edges will have an abrupt change in the microenvironmental conditions at the soil level, whereas in the case of soft edges this change is gradual. I hypothesised that the oak regeneration processes (most of them related to the microenvironment at the soil level) would vary along the forest-edge-grassland gradient, but this change would depend on the edge type. In hard edges the response variables would change abruptly and diverse edge effects will be recorded (negative or matrix effects: Fig. 1.3). In the case of soft edges response variables will change gradually or no edge effects will be recorded (soft edge or no edge effect: Fig. 1.3).

Project structure

To test the general hypothesis I focussed on acorn removal, dispersal, germination and seedling establishment and predation along the forest-edge-grassland gradient using replicated sites with two different edge types in the study area. Acorn production varies considerably from year to year therefore this was included because it is a determinant factor of small mammal abundance and distribution and therefore affects acorn removal (Fig. 1.4).

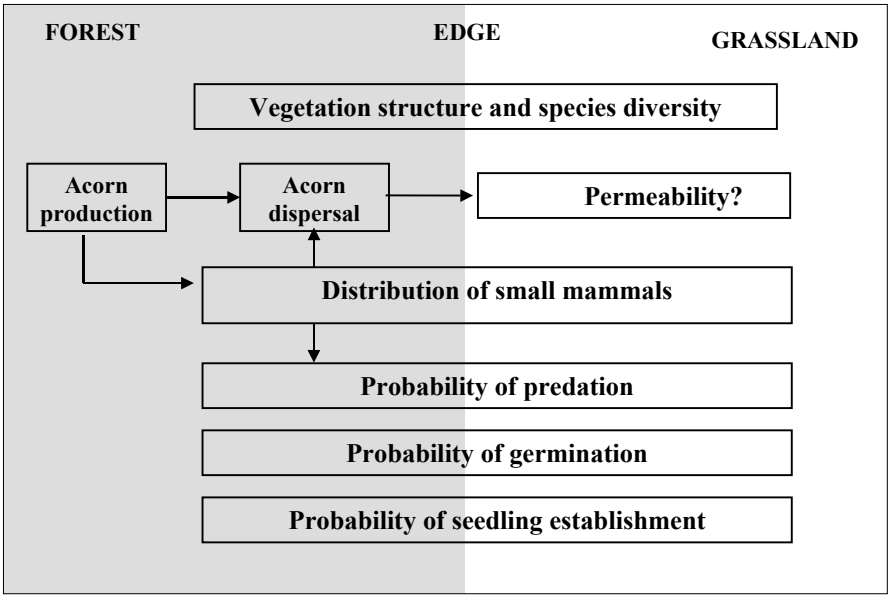

Fig. 1.4 Schematic representation of the study processes.

The main question of this dissertation is how edge structure is affecting oak regeneration processes along the forest-edge-grassland gradient and what are the implications for oak expansion into open areas. The chapters address different aspects of oak regeneration and have therefore been presented as individual papers. Overlap of information was avoided when possible. An overall integration of the results is presented in the final chapter. The thesis is divided into the following sections:

- Chapter 2 presents a description of the study area and experimental sites and assesses the variation in vegetation structure and composition along forest interior-edge-exterior gradients. This part of the study was also designed to evaluate the magnitude of the changes between the forest edge and the adjacent vegetation in order to define edge types. This chapter documents how the patterns of vegetation variables are the result of complex interactions of factors that mask the edge effect and highlights the need for experimental research on regeneration processes.

- Chapter 3 estimates the importance of small mammals relative to other animals as acorn predators and/or dispersers and evaluates the importance of

the microhabitat on their foraging preferences. This chapter is a test of the conceptual model that integrates edge permeability and structure considering the flux of acorn predators and/or dispersers from the forest into openings. I hypothesised that small mammals that are acorn consumers in hard edges will avoid approaching the edge because they will perceive a higher risk of being predated, whereas soft edges will be permeable to these animals resulting in acorn dispersal into the open area (Fig 1.5). Experimental data were obtained to address the following questions:

1. Are there differences in acorn removal across the forest-edge-grassland gradient and in each edge type?
2. How is the edge permeability to acorn dispersers linked with the edge structure?
3. Is masting by oaks determining different spatial and temporal patterns in acorn removal by small mammals on the ground?

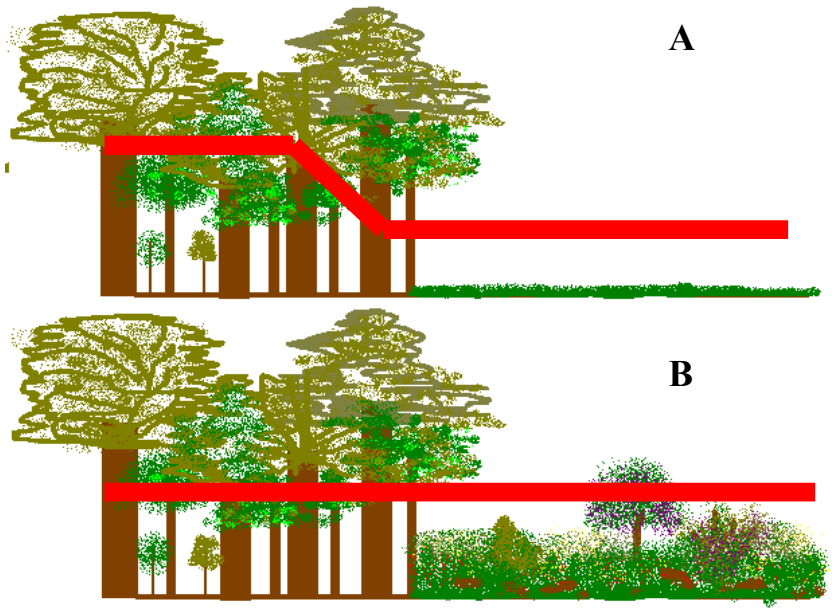

Fig. 1.5 Response variables (red lines) in the forest-edge-grassland gradient in two edge types, A) hard edges created by the sharp contrast between forest and a permanent grassland, and B) soft edges created by the low contrast at the soil level between forest and an abandoned grassland.

- Chapter 4 estimates the relative importance of arboreal rodents as acorn consumers along edge-forest gradients and investigates if these differences

are influenced by the adjacent land use. Experimental data addressed the following questions:

4. Is the adjacent land use affecting distance-from the edge related acorn removal patterns within the forest interior?
5. Do oak species with different timing of germination have different probabilities of being removed?

- Chapter 5 presents an acorn germination test in the laboratory and an experiment in the field using three oak species to evaluate acorn germination across the forest, edge and grassland habitats in the two edge types. Key questions that were addressed include:
    6. How do different habitats (forest, edge and grassland), in both edge types, affect acorn germination?
    7. Are there differences in acorn germination between species belonging to different subgenera?
    8. To what extent does the presence of leaf litter cover in each spatial position affect the acorn germination?

- Chapter 6 describes an experiment that evaluates seedling establishment of five oak species along the forest-edge-grassland gradients in both edge types. Key questions that were addressed include:
    9. How does the structure of the vegetation across forest-edge-grassland gradients in each edge type affect seedling establishment and the incidence of seedling predation?
    10. Are there differences in the seedling performance between species?

Finally, Chapter 7 is a synthesis of the findings. I present the answers to the ten main questions of this research based on the data obtained, followed by a summary of the results in each chapter to determine the net effects of different edge types on oak regeneration across the forest-edge-grassland gradients. I discuss the utility of these findings for management of secondary succession and restoration of montane forests. I also indicate some directions for future research.

CHAPTER 2: Edge effects on plant diversity and vegetation structure in a forest mosaic in the Highlands of Chiapas, Mexico.

ABSTRACT

Forest edges created by scattered-patch clear-cutting have become a common landscape feature in neotropical montane forest. A study was carried in the Highlands of Chiapas, Mexico in order to assess changes in vegetation structure and floristic composition along a gradient from the interior of the forest into adjacent clearings. At six sites an 80 x 10 m belt transect was established perpendicular to the forest/pasture edge. Plant species presence was recorded and seedling, sapling and tree stem diameter and height were assessed. A single-factor (distance) analysis of variance showed no significant effect of distance from the forest interior towards the edge in plant density and basal area ($P>0.05$). Richness and floristic composition did not vary with the depth-of-edge influence (Chi-square tests, $P>0.05$). The level of disturbance may be influencing the response of the vegetation to the edge to interior gradient, and hence the observed results can be explained by the interaction of low but frequent human disturbance and fragmentation. Abandoned grasslands showed the presence of patches of secondary shrub vegetation and recovering forest up to 20 m into the grassland. Expected spatio-temporal changes include the evenness of the forest/grassland edge as time advances. Results suggest that edge effects on vegetation are not measurable with conventional methods where forests are mosaics with small clearings (0.5-2 ha) and widespread, low and frequent human disturbance.

INTRODUCTION

It is now widely appreciated that habitat fragmentation is one of the main factors responsible for loss of species in many areas (Turner 1996). Fragmentation of many tropical forest ecosystems has occurred in recent decades as the result of human activities such as agriculture and timber harvesting. In forested landscapes undergoing fragmentation, as forest areas become divided into increasing numbers of smaller patches, fewer of the patches are able to maintain conditions associated with

the interior of an intact forest, and therefore habitat patches influenced by the effects of edges become a more dominant landscape feature (Ochoa-Gaona & González-Espinosa 2000; Ochoa-Gaona 2001; Ochoa-Gaona *et al.* 2003).

Edge effects in forest mosaics usually result from interactions between forest remnants and adjacent agricultural land or secondary regenerating vegetation. In comparison with forest interior conditions, forest edges are generally characterised by higher light transmittance (Jose *et al.* 1996; Newmak 2001), higher air and soil temperatures (Jose *et al.* 1996; Didham & Lawton 1999), lower relative humidity (Jose *et al.* 1996; Didham & Lawton 1999; Gehlhausen *et al.* 2000), increased wind forces (Laurance 1997), lower availability of soil organic carbon, total nitrogen and phosphorus (Jose *et al.* 1996) and lower soil and litter moisture (Williams-Linera 1990a; Williams-Linera 1990b; Williams-Linera 1993; Jose *et al.* 1996; Saunders *et al.* 1999; Didham & Lawton 1999).

Microclimatic variables differ in the degree and the distance over which, they show an edge effect (see review in Murcia 1995). Factors such as cardinal direction (edge aspect) affect the gradients in environmental variables by influencing the amount of exposure to solar radiation and the physiognomy of the edges (Wales 1972; Matlack 1994; Honnay *et al.* 2002). The type of adjacent land use may also ameliorate the effect of aspect, for example edges bordered by open grasslands or agricultural fields experience more extreme change in microclimatic conditions than dense, multilayered edges bordered by saplings or shrubs that can seal off internal forest conditions from the open adjacent land (Didham & Lawton 1999; Gehlhausen *et al.* 2000). Other factors such as the size of the forest patches and the time of measurement also affect the edge influence on microclimatic variables (Saunders *et al.* 1999). This variation in edge maintenance and aspect affects the depth of edge influences on plant communities (Ranney *et al.* 1981; Matlack 1994; Mesquita *et al.* 1999; Matlack 1994).

Vegetation modification resulting from habitat fragmentation has been extensively studied in a large variety of forest types with different edge characteristics and

surrounded by different vegetation. Studies of edge effects have focused on changes in residual forest structure and species composition associated with forest boundaries and the forest interior (Murcia 1995). A variety of tropical and temperate-zone studies of edge effects have reported the following characteristics near the edge: a) higher species richness (Ranney *et al.* 1981; Lopez de Casanave *et al.* 1995; Oosterhoorn & Kappelle 2000; Gehlhausen *et al.* 2000), b) increased stem densities of shade-intolerant species (Ranney *et al.* 1981; Williams-Linera 1990a; Lopez de Casanave *et al.* 1995), c) increased basal area of trees (Williams-Linera 1990a), d) increased tree mortality (Williams-Linera 1990a; Chen *et al.* 1992; Mesquita *et al.* 1999), e) increased plant growth rates (Williams-Linera 1990b; Chen *et al.* 1992), f) differences in tree seedling density or composition (Gysel 1951; Chen *et al.* 1992; Turton & Freiburger 1997; Benitez-Malvido 1998; Goldblum & Beatty 1999; Harper & MacDonald 2001), g) increased seed germination (Williams-Linera 1990b), h) increased recruitment rates of trees (Laurence *et al.* 1998), i) increased seed bank species richness (Ramírez-Marcial *et al.* 1992), j) increased shrub cover (Matlack 1994; Lopez de Casanave *et al.* 1995) and k) decreased canopy height (Didham & Lawton 1999; Oosterhoorn & Kappelle 2000). It may be the case that these edge-related responses could be specific to particular functional groups of species (i.e. shade tolerant and intolerant species) as reported in several studies (Matlack 1994; Lopez de Casanave *et al.* 1995; Jose *et al.* 1996; Goldblum & Beatty 1999; Gehlhausen *et al.* 2000; Harper & MacDonald 2001; Euskirchen *et al.* 2001).

Although edge effects have been investigated in a large number of different forest areas, very little previous research has been undertaken in neotropical montane forests despite their globally recognised conservation importance (Myers *et al.* 2000). Many montane forest landscapes in Mexico and Central America, such as those in the Mexican state of Chiapas, are characterised by a mosaic of small-interconnected patches of forest and agricultural clearings resulting from intensive patterns of land use (Ochoa-Gaona & González-Espinosa 2000; Ochoa-Gaona 2001), which have developed over centuries or even millennia (Nigh 1975). Previous research has indicated that different edge types may usefully be differentiated, dependent on the pattern of surrounding land use and the degree of edge abruptness

(Ranney *et al.* 1981; Didham & Lawton 1999); these different edge structures may affect the boundary permeability and therefore the movement of organisms and fluxes (i.e. exotic weeds into the forest) across the two habitats (Wiens *et al.* 1985; Cadenasso & Pickett 2001; Honnay *et al.* 2002; Piper *et al.* 2002).

The objectives of this study were to assess the characteristics of forest edges in the montane forests of Chiapas, Mexico. Although a number of detailed descriptions of plant communities have been made of the forest in the Highlands of Chiapas (2020-2560 m), the structure and importance of edges has never previously been assessed in these forests. This study was designed to: a) evaluate the magnitude of the changes between the forest edge and the grassland vegetation in order to define edge types, and b) assess the variation in vegetation structure and composition along forest interior-edge-exterior gradients. It was hypothesised at the outset of this study that, on the basis of research obtained in other forest types, the relative abundance of early successional species and tree seedlings will be higher near the edge (0-10 m into the forest) because habitat edges may provide some degree of protection from frost, while providing high light availability. Many previous studies dealing with the characterisation of edge effects have suffered from pseudoreplication, in that the plots or transects were positioned in the same forest edge (Murcia 1995), reducing the confidence that can be placed in the results. In this study edges were therefore located in different clearings to provide independent replicates.

METHODS

Study area

The study area is located in the Highlands of Chiapas (2020-2560 m), in southern Mexico (Fig. 2.1). The area (about 11 000 km^2) contains various forest formations in a complex landscape with high biodiversity resulting from interactions among geological, edaphic, climatological and anthropogenic factors (Collier 1975; Breedlove 1981). The region contains about 131 families, 489 genera and 980 species, subspecies or varieties of vascular plants. Approximately 27 to 30% of these

species are characteristic of montane cloud forest, making it an important area for conservation (González-Espinosa *et al.* 1997). The dominant vegetation consists of patches of diverse secondary plant communities associated with pine-oak forests, interspersed with pastures, agriculture and, on the higher peaks, neotropical montane cloud forest (Breedlove 1986; González-Espinosa *et al.* 1991; González-Espinosa *et al.* 1995). The climate is temperate sub-humid (mean annual temperatures are 13-17° C), with a summer rainfall regime (annual rainfall is 1100-1600 mm, with more than 85% occurring from May to October; Fig. 2.2) and occasional severe winter frosts in open areas at high elevations (>2200 m). The most common soils are dark-brown, shallow to moderately deep (30-100 cm) clays and clayey loams (leptosols and cambisols associated with phaeozoms and regosols). The soils are poorly developed and most of them have a neutral to alkaline pH owing to their calcareous parent material (Parra-Vázquez 1989; Mendoza-Vega *et al.* 2003).

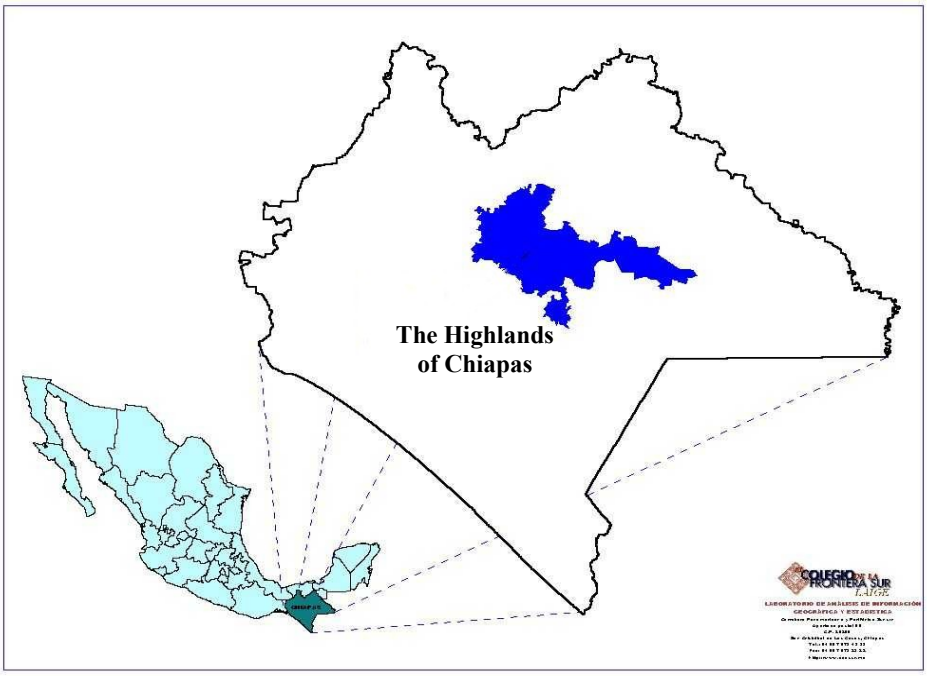

Fig. 2.1 Location of the Highlands of Chiapas (1500-2700 m) in southern Mexico.

The Highlands of Chiapas have been intensively managed by indigenous Mayan populations (Tzotzil, Tzeltal and Chol speaking) for centuries with slash and burn ("Milpa") systems. A detailed description of the land use is presented in Chapter 1.

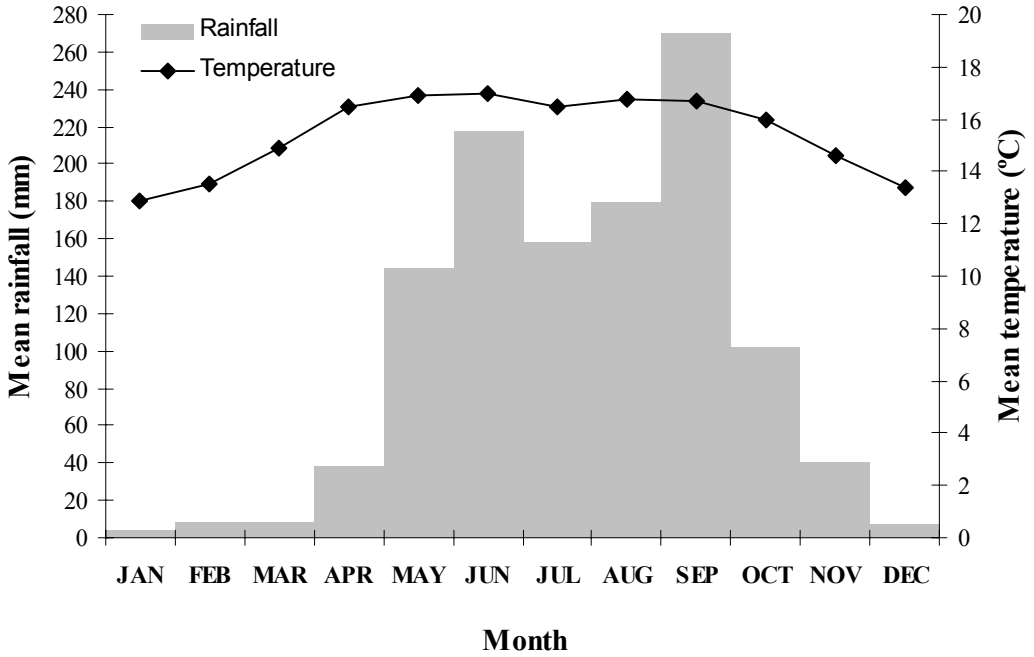

Fig. 2.2 Mean monthly rainfall (mm) and temperature (º C) from January 1994 to May 2002 at the meteorological station Chilil (latitude N 16º 40'30'', longitude W 92º 29'10'' and altitude 2200 m), Huistan municipality, Chiapas, Mexico. Data obtained from the National Water Commission of Mexico.

This type of agriculture takes advantage of the process of secondary succession, as areas of forest cleared for agriculture are allowed to regenerate naturally to forest during fallow periods. In this way, the amount of forest clearance can be balanced to meet the needs of a stable human population. However, as has occurred in many other neotropical areas, the human population has increased rapidly in recent decades (substantially higher than the national population growth rate). As a consequence, the long fallow periods of the original "Milpa" rotation have been severely shortened, leading to a highly disturbed landscape that includes clearings of cultivated land, secondary forest (or tree and shrub fallow), temporary and permanent grazing lands, and disturbed forest (González-Espinosa *et al.* 1995; De Jong *et al.* 1999). Other human disturbance in the study area includes: harvesting of saplings for firewood extraction, lopping of adults, occasional logging of selected trees (including illegal logging), chicken foraging with consequent disturbance of tree seedlings and the forest floor and occasional browsing of seedlings and saplings across the forest edge by livestock. Canopy gaps associated with windthrows and logging of selected trees represent areas of localised secondary succession within the forests.

Study sites

The study was conducted in Rancho Merced Bazom located in Huistan municipality. Land (approximately 22 ha) is individually owned by three farming families whose first language is Tzotzil. Logging and agricultural activities have produced a mosaic of openings ranging from 0.5 to 2 ha at varying stages of regeneration within the pine-oak forest matrix. Past and recent land-use patterns in Rancho Merced Bazom are similar to those in Huistan Municipality (see detailed description in Chapter 1) resulting in a forest mosaic (Fig. 2.3) with scattered clearings derived from Milpa, used as permanent or temporal grasslands and forest in different successional stages (secondary succession is described in Chapter 1).

During a reconnaissance survey in May 2000, six representative sites were chosen on the basis of the presence of clearings with different grazing pressure within a matrix of mature pine-oak forest and the availability of permission from the owners to conduct field research. Replication is highly desirable because of site heterogeneity. Three of the clearings adjacent to the forest were selected as heavily grazed sites and three presented a more complex structure with scattered presence of shrubs and tree saplings (see Chapter 3). The sites were geo-located using a GPS (Garmin Inc. Olathe, USA). Distance between sites is highly variable (200-750 m; Fig. 2.3). The sites were named after their owner's initials (Table 2.1), PM (Pedro Martínez), MD (Manuel Díaz), NM (Nicolás Martínez), PP (Pedro Pérez), NP (Nicolás Pérez) and MP (Miguel Pérez). The age of the forest edge (time elapsed since the forest was cut) and the disturbance history was determined by questioning the site owners and local farmers.

The process of edge creation was similar in all the sites. The traditional "Milpa" system begins with the cutting of small areas (0.5 to 2 ha) of pine-oak forest (for more details see Nigh (1975)). The land is burned during March and April (at the end of the dry season) to destroy roots and seeds of undesirable weeds. Crops are seeded when rain becomes frequent (May-June) to stimulate germination before seeds are predated. At the beginning of the dry season (October-November) when leaves, stalk

and husk are dry, the corn and the beans are harvested. Once the crop is abandoned, secondary succession develops (González-Espinosa *et al.* 1991).

This recovery process can be accelerated by resprouting from stumps of tree species such as oaks and by the nearby availability of propagules in a matrix of vegetation types (Ramírez-Marcial *et al.* 1992). This system implies continuous successional changes, as the secondary forest can be logged and burnt again to establish the crop (Ochoa-Gaona & González-Espinosa 2000). During the fallow, clearings may be used as sporadic or permanent grasslands. Cattle may enter into the forest crossing the edge of the forest patches.

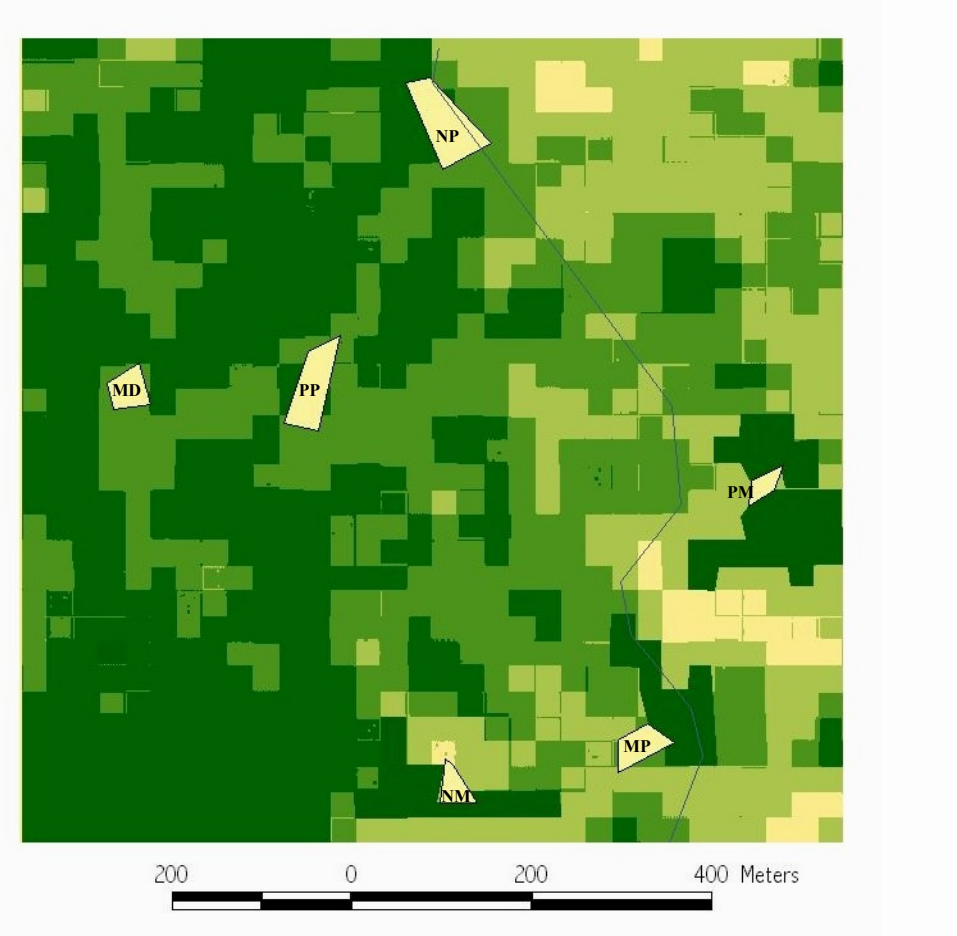

Fig. 2.3 Map of the clearings used as experimental sites in Rancho Merced Bazom, Huistan, Chiapas. Experimental plots were overlapped on a Landsat satellite image (2000) provided by LAIGE, ECOSUR. ArcView GIS v. 3.1 was used to convert the image to a grid theme with four categories based on a gradient of vegetation cover from dense vegetation cover (dark green) to open areas (yellow).

Table 2.1 Description of six edges studied in the Highlands (1500-2700 m) of Chiapas, Mexico. Patch position and size were calculated using a GPS. Slope was calculated in the open area adjacent to the forest patch.

Edge name	Altitude (m)	Latitude N	Longitude W	Aspect of forest edge	Slope (°)	Open area size (m^2)
PM	2410	16°44'23.2''	92°29'12.3''	E	38	800
MD	2370	16°44'26.7''	92°29'35.8''	W	19	1601
NM	2380	16°44'25.7''	92°29'24.2''	NE	11	1128
PP	2468	16°44'25.7''	92°29'29.9''	S	16	3352
NP	2440	16°44'37.0''	92°29'26.3''	E	45	4448
MP	2400	16°44'15.0''	92°29'15.6''	SW	16	1769

The needs of the indigenous inhabitants for food, fuel, medicines and timber are mainly met by plant products obtained from the open fields, fallows and forests. Pine trees are cut for timber production (over 15-20 cm DBH), while oak trees are used for fuelwood and making charcoal (over 8-10 cm DBH) (González-Espinosa *et al.* 1995). Most of the larger pine trees (>30 cm DBH) were exploited in the past (1970) by a logging company, except in the forest in the site PM. In all the forested areas, hunters shoot deer, squirrels and a variety of other animals and birds for food. The structure and composition of the forest interior studied in the present work has been described in detail already (González-Espinosa *et al.* 1991; González-Espinosa *et al.* 1992; González-Espinosa *et al.* 1995; González-Espinosa *et al.* 1997; Galindo-Jaimes *et al.* 2002).

Study design

From April to June to 2000 a detailed study was carried out along the forest edges in order to assess the edge effects on the overall vegetation and the characteristics of edge vegetation. In each of the study sites an 80 m long and 10 m wide transect was established perpendicular to the edge, running from the forest (60 m) through the edge into the forest exterior (20 m into the grassland). Transect length and position were determined by the scale of heterogeneity within forest fragments and clearing sizes to avoid the effect of the opposite edge of the clearing. The edge was defined as

the line coinciding with the bases of bordering mature (>30 cm DBH) tree stems (Jose *et al.* 1996; Oosterhoorn & Kappelle 2000). Within these belt transects, all the woody plants, shrubs and seedlings were counted within contiguous plots of 10 x 10 m. In each of these plots four stem size categories in different sized nested sub-plots were identified: 1) seedlings: <50 cm height (1 x 1 m; sub-plot), 2) small saplings: 50-150 cm height (2 x 2 m), 3) large saplings: >150 cm height and DBH <5 cm (5 x 5 m) and 4) trees: >5 cm DBH (10 x 10 m). Species were identified according to standard taxonomic reference works (Breedlove 1981; Breedlove 1986); nomenclature follows these same sources (Appendix 1: Tables A.1.1 and A1.2). Basal stem diameter was measured in seedlings; DBH values were assessed for large saplings and trees. In addition, the line-intercept method (Mueller-Dombois & Ellenberg 1974) for measuring cover was used to characterise the grassland vegetation. A 10 m long measuring tape was laid out (at 12 and 24 m parallel to the edge) and the leaves or stems that overlapped or intercepted the line were recorded by species. The accumulated length occupied by any one species was expressed as the percent of the total tape length as cover for that species. When there was a second stratum (>50 cm in height) over the prostrate herbaceous layer, the height, cover and composition of the shrubs or herbs were also registered.

Recent human disturbance was evaluated at each site by counting and measuring stumps of trees that had been logged in recent years and by counting and measuring the length of trails (human and livestock trails) within the forest. The six sites were classified according to a relative disturbance index. Number of stumps, stump diameter, number of trails, trail width, number of trees with branch extraction evidence and number of animal faeces were summed. The total was transformed into a percentage of the highest value obtained and the percentage was transformed into a categorical value with three levels (low: 0-33%, medium: 33-66% and high: 66-100%). Canopy openness (at 1.5 m above the soil) was estimated at the centre of each plot using a spherical densiometer (Forestry Suppliers Inc. Batlesville, Oklahoma, USA). The average height of canopy trees was obtained using a clinometer (Suunto PM 5/360PC, Finland); the height of five randomly chosen trees

was measured at the edge and additionally, five trees situated 40 m into the forest were also measured.

In order to characterise the light environment at the forest floor in these permanent plots, two parallel line transects (50 m long, 20 m apart) running across the forest-edge-pasture gradient (30 to -20 m) were positioned in each study site. Fifty continuous readings of photosynthetically active radiation (PAR μmol m^{-2} s^{-1}) were taken along each 10-m section of the transect during one clear day and then averaged to one value per section using a ceptometer (Decagon, Pullman Washington, USA) placed 10 cm above the soil. The ceptometer measures mean PAR incident on 80 evenly spaced sensors along a narrow sampling bar (80 cm long). Additionally, in the same locations, total vegetation cover (10 cm above soil surface) was estimated using a spherical densiometer.

Statistical analysis

Data were divided into two groups. The first was used to investigate whether the edge proximity had an effect on forest interior vegetation (edge effects) by comparing the plots located along the gradient (0 to 60 m). The second group was used to characterise the forest edge vegetation transition (seedlings, saplings and large saplings) into the grasslands (0 to -20 m). Dependent variables were basal area, stem density (after $\log_{10} + 0.25$ transformation) and canopy openness (after arcsine square root transformation) (Sokal & Rohlf 1998). Single-factor analysis of variance was used. The independent variables were plot location along the gradient and site. Tukey's HSD multiple comparisons were used to detect significant differences among plots means (SPSS v.10.0.1, SPSS Inc.).

In order to describe the forest edge and forest interior vegetation, importance values were calculated using stem density and basal area (stem density + basal area), importance values were obtained for each life form for each species within the forest (20 to 60 m) and in the edge (0 to 10 m). Relative importance values (RIV) were calculated by summing the importance value for each species in each life form

(seedlings, small saplings and shrubs, large saplings and trees) and transforming the value into percentage of the highest value recorded (Mueller-Dombois & Ellenberg 1974). Plant species diversity was calculated in each of the study sites and each plot (distance from the edge) using Shannon-Wiener's diversity index ($H = -\Sigma (p_i) (\ln p_i)$, where p_i is the proportion of individuals in the ith species) and Evenness index ($J = H / \ln (S)$, where S is the total number of species in the habitat). These indices were calculated using Species Diversity and Richness (PISCES v. 2.3, Conservation Ltd. Oxford, UK). Significant differences in species diversity and evenness between plots (distance from the edge) were examined using single-factor ANOVA. In addition, plant species were placed in one of three categories according to their shade tolerance and successional stage: 1) early-successional species, 2) mid-successional species and 3) late-successional species. Species were categorised according to González-Espinosa *et al.* (1991 and 1997). These data and the total number of species recorded were analysed using chi-squared goodness of-fit tests as a function of plot position along the gradient (SPSS v.10.0.1). All full ANOVA tables are presented in Appendix 1 (Tables A.1.3-A.1.21) in the same order as they were reported in the results section. Variation about the mean is reported as mean ± 1 SE, unless otherwise specified. Negative distances indicate metres from the edge into the grassland.

RESULTS

Vegetation structure and composition

Mature forest was vertically structured into three layers. The forest canopy (25-40 m) was dominated by *Quercus laurina* (RIV=27.7%), *Pinus tecunumanii* (18.9%) and to lesser extent *Q. crassifolia* (6.9%), *Cleyera theaeoides* (5.8%) and *Persea americana* (5.7%). Bromeliads, orchids, and epiphytic ferns cover most of the large branches. There was a continuous understorey layer (5-25 m) mostly dominated by *Rapanea juerguensenii* (RIV=23.9%), *Oreopanax xalapensis* (13.6%), *P. americana* (13.1%), *Ternstroemia pringlei* (7.8%), *Ternstroemia lineata* (5.4%), *Symplocos limoncillo* (5.3%) and *Verbesina perymenioides* (4.9%). A dense and diversified small sapling and shrub stratum (89.9 ± 18.5 cm, ± SD in height) included *P. americana* (30.0%),

O. xalapensis (15.1%), *R. juerguensenii* (9.6%), *Solanum nigricans* (6.1%), *T. lineata* (5.1%), *Senecio cristobalensis* (3.0%) and *Eupatorium nubigenum* (2.9%). The seedling stratum (15.6 ± 9.2 cm, ± SD in height) was dominated by *O. xalapensis* (13.5%), *R. juerguensenii* (13.0%), *V. perymenioides* (8.8%), *S. nigricans* (4.9%), *Q. laurina* (5.4%) and *Prunus rhamnoides* (5.4%).

Forest edge vegetation presented a canopy dominated by *Q. laurina* (RIV=20.6%), *P. tecunumanii* (16.6%), *Alnus acuminata* ssp. *arguta* (11.6%), *P. montezumae* var. *montezumae* (11.2%) and to lesser extent *P. pseudostrobus* var. *pseudostrobus* (5.7%) and *P. americana* (5.1%). The understorey and sapling layer was dominated by *R. juerguensenii* (27.1%), *V. perymenioides* (11.3%) *Q. laurina* (10.6%), *O. xalapensis* (8.5%), *P. rhamnoides* (8.0%) and *T. pringlei* (6.8%). A small sapling and shrub stratum (86.2 ± 17.8 cm, ± SD in height) included *R. juerguensenii* (18.8%), *Cestrum guatemalense* (15.9%), *P. rhamnoides* (15.0%), *Fuchsia thymifolia* (11.3%), *V. perymenioides* (8.3%), *S. nigricans* (7.4%) and *Viburnum jucundum* (5.3%). The seedling stratum (10.9 ± 7.0 cm, ± SD in height) was dominated by *V. perymenioides* (16.7%), *O. xalapensis* (15.6%), *Q. laurina* (10.5%), *F. thymifolia* (13.0%) and *R. juerguensenii* (8.1%).

A total of 66 species of 41 genera belonging to 32 families were recorded. From this list, two species (*Arbutus xalapensis* and *Fuchsia encliandra*) only occurred in forest edges (0-10 m). The other species that occurred near forest edges (0-10 m) were present also in the forest interior while 22 species (including some late-succesional species as *Clethra suaveolens*) only occurred within the forest interior (20-60 m from the edge). Within the forest, total species richness (number of species) and diversity (*H*) varied between the sites, 39 species were recorded in MD (*H*=2.9), 37 in PP (*H*=3.1), 35 in NM (*H*=2.8), 30 in PM (*H*=2.8), 30 in NP (*H*=2.7) and 29 in MP (*H*=2.4).

In all the sites the owners have allowed the entrance of livestock into the forest interior. Edge maintenance and structure are the result of the pattern of land use since the edge was created. In only one site (PM), the owner removed edge vegetation (30

years ago) to maintain the original patch size, but left pine and oak saplings. There was no evidence of fire penetrating the forest edges at any of the study sites. All the grasslands were previously the sites of crop cultivation under the traditional slash and burn system (fallow periods lasting from 13 to 50 years), but the length of the period that these areas were cultivated varied between the sites (Table 2.2). Herbs with varying height and density covered the ground of the open patches in each site. Based on the information provided by the owners and the grassland structure, it can be concluded that on the grasslands of the sites PP, NP and MP, grazing by livestock has been more intense (4-8 head of cattle per patch during all over the year) than in the grasslands of the sites PM, MD and NM (3-8 head of cattle only during the dry season).

Table 2.2 Disturbance regime and land-use history of six study sites in the Highlands (1500-2700 m) of Chiapas, Mexico. The information was obtained from interviews with the owners of the sites. Forest disturbance was estimated with a categorical index. Tree height (mean ± 1 SE) was evaluated from five trees in the forest edge and five in the forest interior in each site.

Edge name	Edge age (years)	Milpa period (years)	Years since the last cultivation	Grazing period (years)	Edge tree height (m)	Forest tree height (m)	Forest Disturbance
PM	>60	3	13	13	30.1±6.7	19.0±2.5	Low
MD	34	12	13	6	18.8±3.9	27.7±3.9	High
NM	>30	5	30	30	25.5±8.1	25.1±2.5	Medium
PP	51	33	14	14	17.6±2.6	22.0±2.7	Medium
NP	>60	1	50	49	21.3±2.1	22.3±3.6	High
MP	>30	-	>17	13	27.9±0.7	18.6±1.4	High

In site PP, one prostrate herbaceous stratum (18.0 ± 7.9, ± SD cm in height) covers all the area, and it is dominated by graminaceous species (20%), *Alchemilla pectinata* (38%), *Alchemilla aphanoides* (8%), *Geranium vulcanicola* (5%), *Bidens ostruthioides* (4%) and *Ranunculus petiolaris* (4%). Saplings and regeneration of *R. juerguensenii, Prunus serotina, P. tecunumanii* and *Q. laurina* (1.6 individuals

m^{-2}) were distributed along the edge and up to 7.5 m from the edge. In NP, a prostrate herbaceous stratum (10.2 ± 3.6 cm) covers all the area, and is dominated by gramineous species (70%), *Prunella vulgaris* (12.5%) and *Hediotys serphyllacea* (6.2%). In MP, 100% of the area is covered by a prostrate vegetation layer (14.9 ±9.9 cm) dominated by gramineous species (25%), *H. serphyllaceae* (19%), *B. ostruthioides* (10%), *Stevia ovata* (9.8%) and *A. aphanoides* (7.5%). In this grassland also, *Q. laurina, P. tecunumanii* and *P. serotina* seedlings (0.2 individuals m^{-2}) were distributed along the edge and up to 10 m from the edge. Pine saplings here are tall enough not to be affected by browsing and browsed saplings of oaks survive through resprouting after being browsed.

Sites PM, MD and NM had grasslands with at least two vegetation layers. These sites had not been grazed intensively by livestock. In PM there is a tall (0.5 to 1.5 m) herb and shrub stratum covering 60.0 ± 40.0% of the area dominated by *Tagetes nelsonii* (20%), *Salvia cinnabarina* (15%) and *Rubus adenotrichus* (6.5%). The prostrate stratum (25.9 ± 10.2 cm, ± SD in height) is dominated by gramineous species (17.6%), *R. petiolaris* (8%) and *G. vulcanicola* (5.5%). Leaf litter covers about 3% of the area.

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In MD the grassland has two layers. The stratum from 0.5 to 1.0 m covers 30.0 ± 10% of the area and is dominated by *R. adenotrichus* (27%). The prostrate stratum (21.6 ± 13.5 cm, ± SD in height) is dominated by gramineous spp. (26%), *H. serphyllaceae* (9%) and *Pteridium aquilinum* (7.5%). Litter and dead wood cover about 3% of the area. Vigorous saplings and regeneration of *P. tecunumanii, Cornus disciflora,* and *Q. laurina* seedlings (0.1 individuals m^{-2}) were distributed from 5 to 21 m from the edge.

In NM, there is an interspersed shrub stratum covering 35.0 ± 35.0% of the area dominated by *Baccharis vaccinioides* and *Monina xalapensis*. Gramineous cover is 6% and there is a tall (30.1 ± 12.5 cm) herbaceous stratum dominated by *Cuphea aequipetala* (30%), *Helenium* sp. (12.6%), *R. petiolaris* (9%) and *G. vulcanicola* (7%). Dead wood covers about 9.5% of the area.

Edge effects

A single-factor (distance from the edge) analysis showed no significant effect of distance from the edge to forest interior on the basal area of large saplings (F=0.86; df= 5, 35; P=0.518) and trees (F=1.03; df= 5, 35; P=0.423; Fig. 2.4). There were significant differences in the total basal area of trees between sites (F=3.59; df= 5, 35; P=0.014). The site PM presented higher mean basal area of trees when compared with site NP and MD (Fig. 2.4). Small sapling, large sapling and tree stem density did not vary with the depth-of-edge influence (ANOVA, P>0.05; Fig. 2.5). However, density of large saplings was significantly (F=5.15; df= 5, 35; P=0.002) higher in the site MP when compared with the other sites (Fig. 2.5). Tree seedling density was not significantly affected by distance from the edge (F=0.90; df= 5, 35; P=0.496; Fig. 2.6). A regression analysis was performed to test if tree seedling density changed with canopy cover but no significant relationship was found (P>0.05; Fig. 2.6).

Canopy openness did not significantly vary with depth-of-edge influence (ANOVA, P>0.05; Fig. 2.6), perhaps reflecting an uneven canopy resulting from frequent treefall gaps in different positions from the edge. Canopy height of the forest interior was rather similar compared with the average height of forest edge trees (single-factor ANOVA, $P > 0.05$). In some sites, trees in the forest edge were taller than trees in the forest interior, (site MP and PM, Table 2.2). This may be attributable to the presence of pines along the edge with higher growth rates than the oaks in the forest interior.

Total number of species was similar along the edge to forest interior gradient (χ^2 =6.04; df=5; P=0.302; Fig. 2.7). Frequencies of species belonging to different successional stages (early-, mid-, and late-successional species) were not affected by distance from the edge (χ^2 =1.83; df=10; P=0.998). Diversity and evenness did not vary as distance from the edge increased (ANOVA, P>0.05). Species richness and evenness showed different patterns as distance from the edge increased in each site (Fig. 2.7).

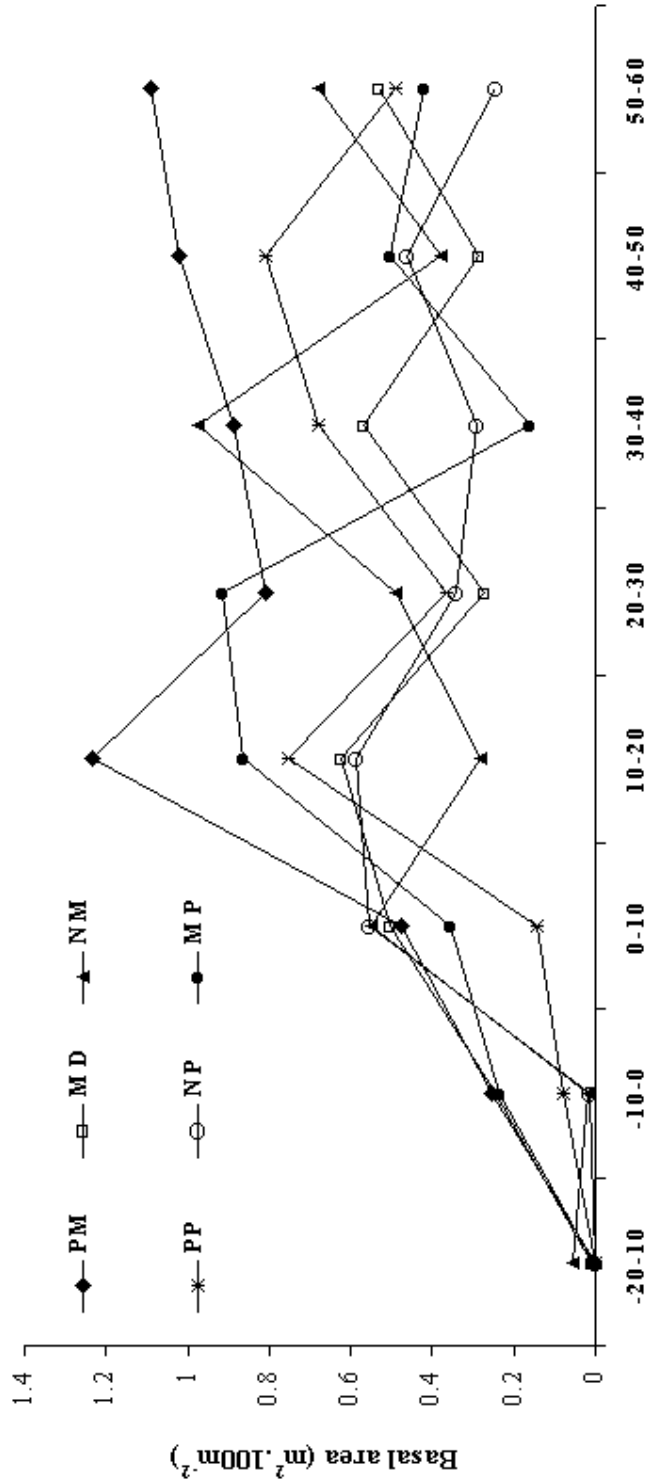

Fig. 2.4 Changes in basal area of large saplings and trees within 10 x 10 m plots positioned along a forest interior-edge-grassland distance gradient at six sites in the Highlands of Chiapas, Mexico. Negative distances indicate metres from the edge into the grassland.

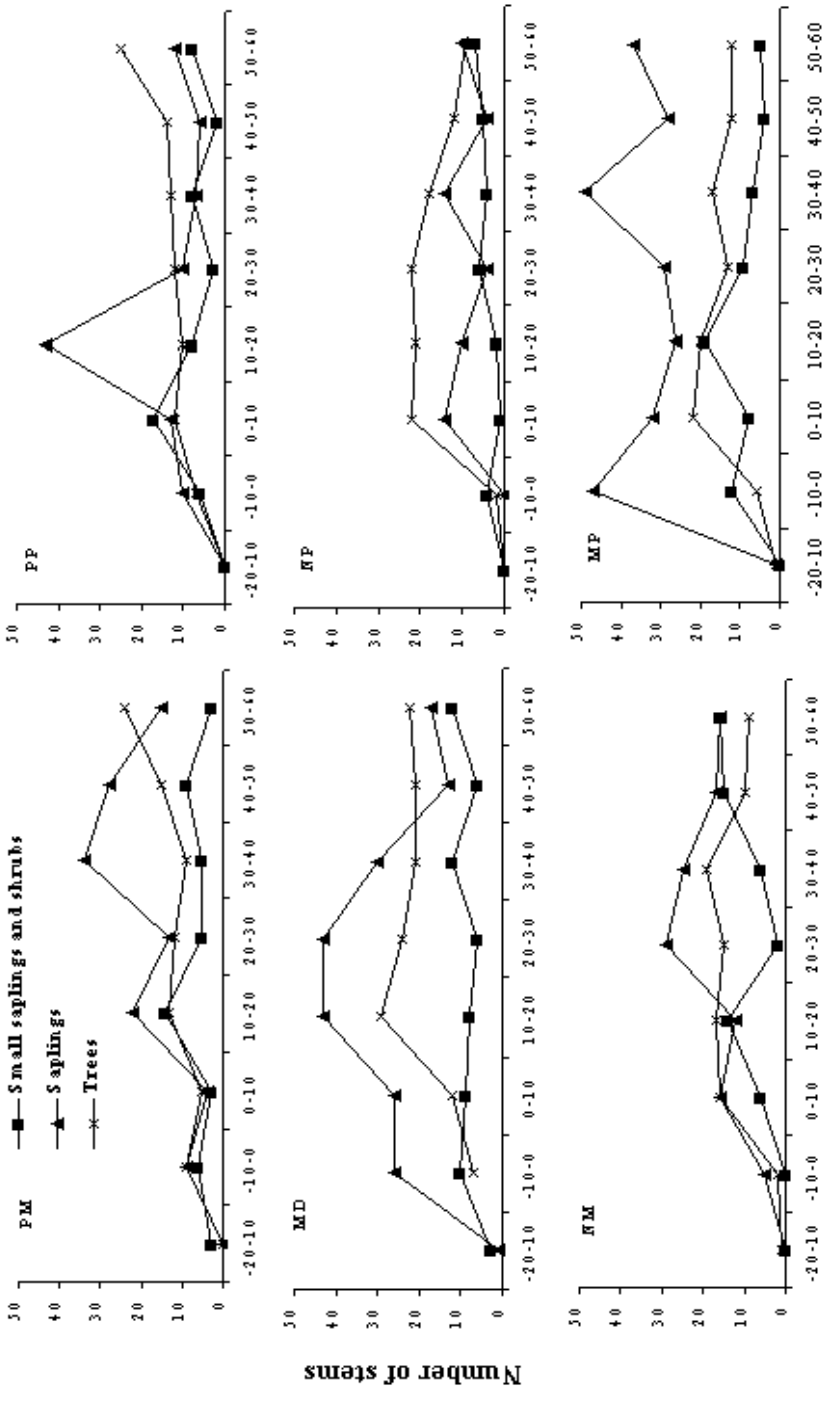

Fig. 2.5 Distribution of stem numbers of small saplings and shrubs (50-150 cm height; 2 x 2 m), large saplings (>150 cm height and DBH < 5 cm; 5 x 5 m) and trees (>5 cm DBH; 10 x 10 m) along a forest interior-edge-grassland distance gradient at six sites in the Highlands of Chiapas, Mexico. Negative distances indicate metres from the edge into the grassland.

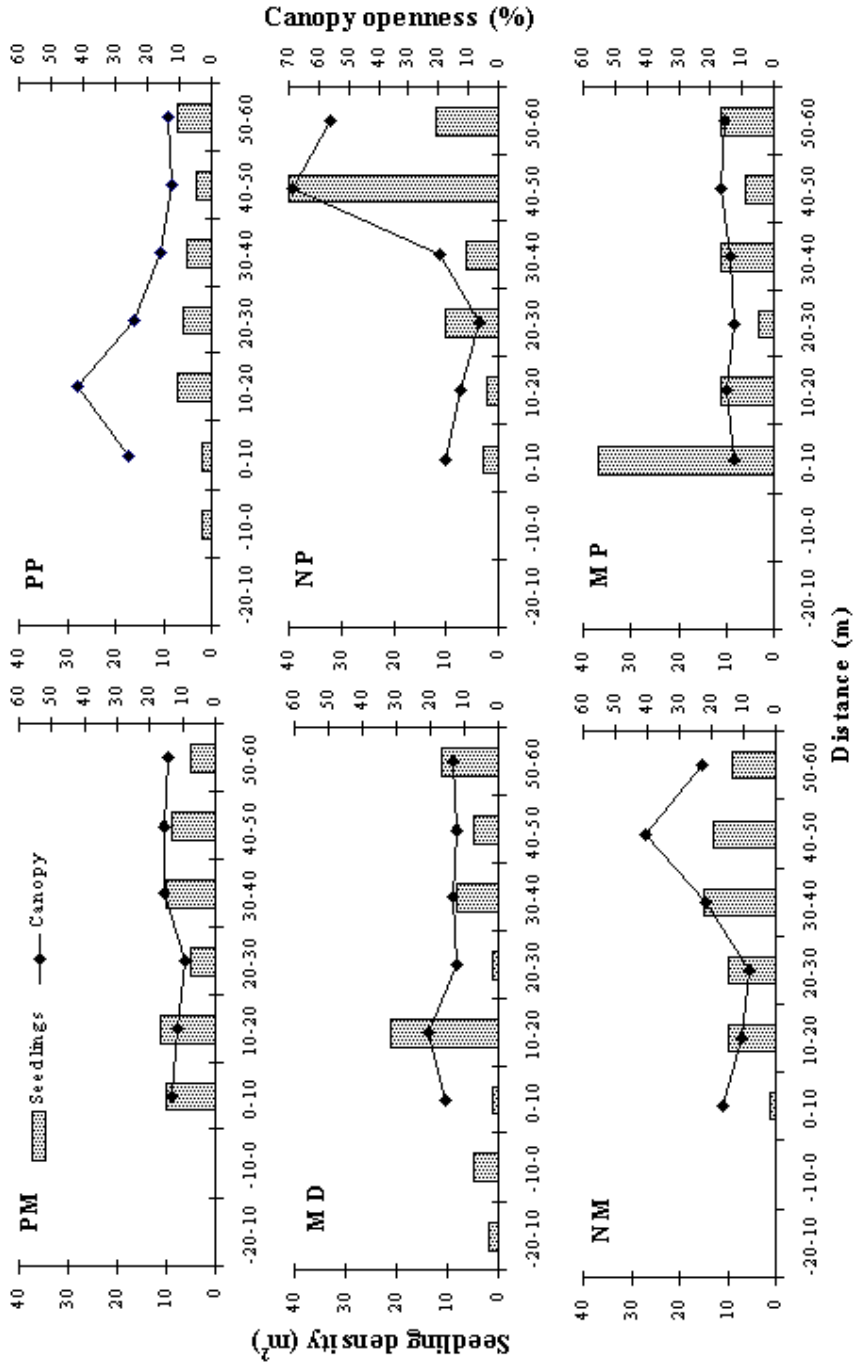

Fig. 2.6 Distribution of tree seedlings (< 50 cm height) per square metre and changes in canopy openness (%) estimated 1.5 m above the soil along a forest interior-edge-grassland distance gradient at six sites in the Highlands of Chiapas, Mexico. Negative distances indicate metres from the edge into the grassland.

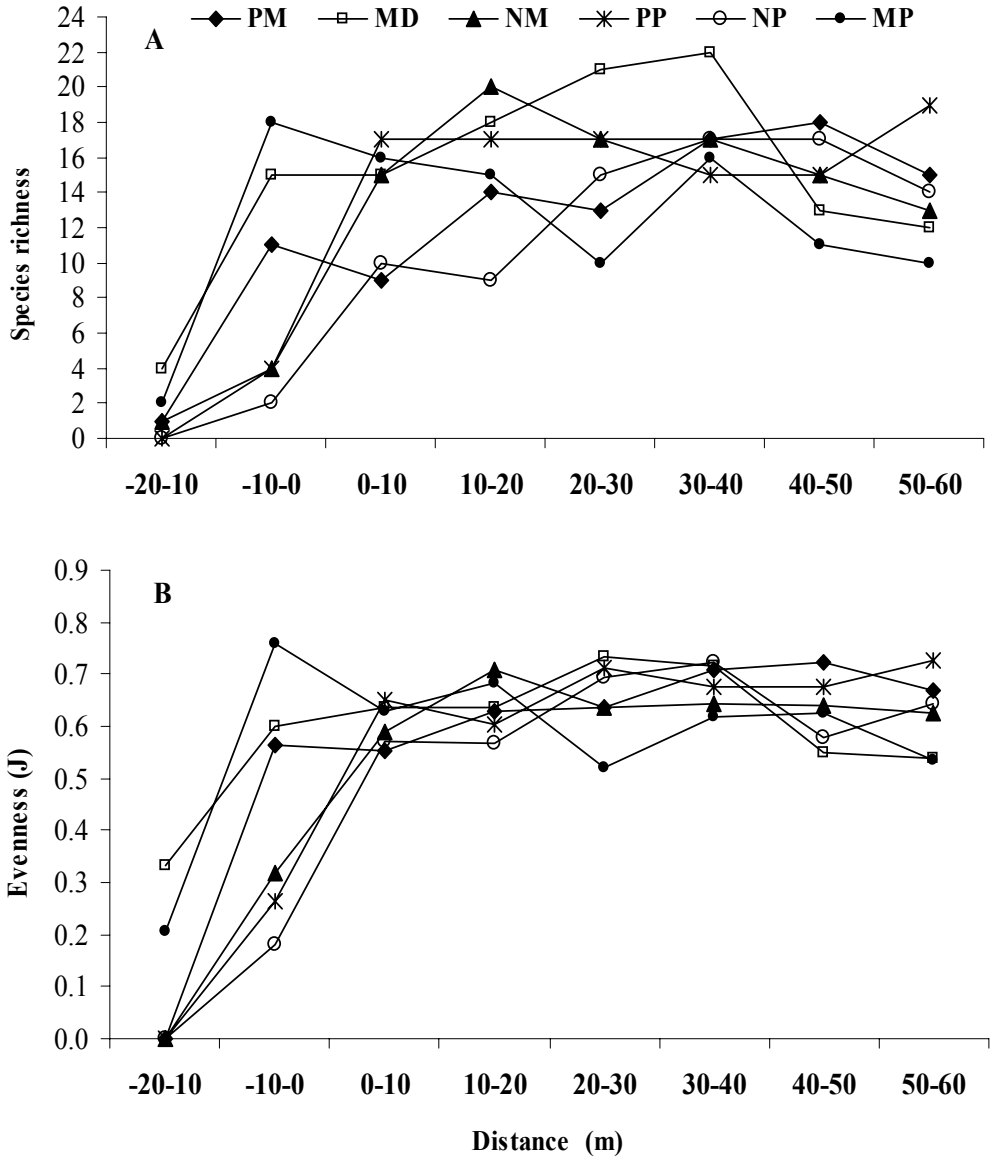

Fig. 2.7 A) Species richness (number of woody species) and B) evenness index (J) for 10 x 10 m plots positioned along a forest interior-edge-grassland distance gradient at six sites in the Highlands of Chiapas, Mexico. Negative distances indicate metres from the edge into the forest exterior.

Edge sharpness

The transition from forest edge to the open area varied between the sites from abrupt (i.e. maintained by grazing at their original location for more than 20 years) to gradual (i.e. tall herbaceous and shrub strata covering the ground up to 20 m from the forest edge). There were no significant differences between the forest edge and the

grassland plots (10 and 20 m from the edge) in large sapling basal area (ANOVA, $P>0.05$). Density of tree seedlings was significantly ($F=4.64$; df=2,10; $P=0.037$) higher in the edge and 10 m into the grasslands (9.0 ± 5.8 and 3.8 ± 1.7 stems m^{-2}, respectively) than 20 m from the edge into the grassland (0.33 stems m^{-2}). The number of stems of small saplings (50-150 cm height) was similar between the forest edge (1.8 ± 0.6 stems 4 m^{-2}) and 10 m into the grasslands (1.6 ± 0.4 stems 4 m^{-2}), but different compared with 20 m from the edge into the grassland (0.2 ± 0.1 stems 4 m^{-2}; $F=5.95$; df=2, 10; $P=0.020$; Fig. 2.5). Stem density of large saplings did not vary between the forest edge and the grassland plots (ANOVA, $P>0.05$). Higher numbers of species were recorded at the forest edge and 10 m into the grassland than 20 m from the edge into the grassland for seedlings ($\chi^2=10.40$; df=2; $P=0.006$), small saplings ($\chi^2=13.28$; df=2; $P=0.001$) and large saplings ($\chi^2=39.93$, df=2, $P<0.001$). Species diversity (H) and evenness (J) were similar in the edge ($H=2.2 \pm 0.1$, $J=0.8 \pm 0.02$) and 10 m from the edge ($H=1.6 \pm 0.3$, $J=0.6 \pm 0.1$), but significantly different (H: $F=33.19$; df=2,10; $P<0.001$; J: $F=25.26$; df=2,10; $P<0.001$) between the edge and 20 m from the edge in the grasslands ($H=0.3 \pm 0.2$, $J=0.1 \pm 0.1$). Frequencies of species belonging to different successional stages (early-, mid- and late-successional species) between the forest edge and grassland plots were not significantly different for tree seedlings ($\chi^2=0.91$; df=4; $P=0.924$) small saplings ($\chi^2=0.62$; df=4; $P=0.961$) and large saplings ($\chi^2=3.48$; df=4; $P=0.481$).

Edge sharpness in each site can be expressed in terms of the PAR reaching the forest floor. In sites PM, MD and NM there was a gradual increase of the light reaching the soil surface within the grasslands as distance from the edge increased (Fig. 2.8). In sites PP, NP and MP there was an abrupt increase at the edge (0 m) of the PAR reaching the soil surface, whereas in sites PM, MD and NM the light environment continued to change until 15 to 20 m into the grasslands. Based on these results, these sites were grouped and PAR reaching the soil surface and canopy openness were analysed as a function of edge type and distance from the edge to see if there were differences between these two groups. Vegetation cover estimated at 10 cm above the soil surface showed a significant interaction between edge types and distances from the edge ($F=4.52$; df=5, 24; $P=0.005$). The effect of edge type on

canopy openness was exclusively due to the values recorded in the grasslands (Fig. 2.8a). PAR was only affected by distance from the edge (F=10.60; df=5,24; P<0.001) but also exclusively due to the values recorded in the grasslands (Fig. 2.8b).

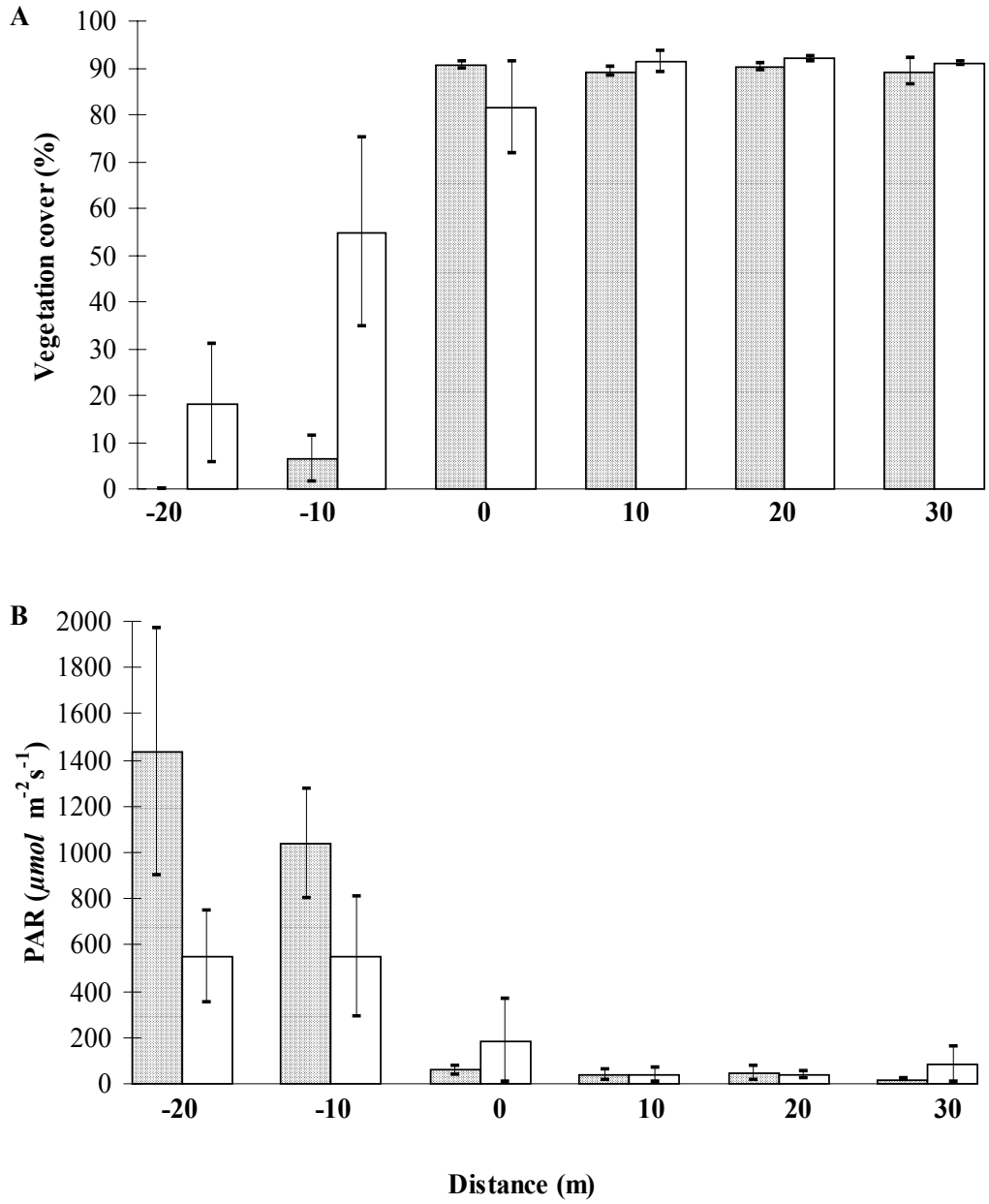

Fig. 2.8 Changes in A) vegetation cover estimated 10 cm above the soil surface and B) PAR reaching the soil surface as a function of distances from the edge. Shaded bars represent sites with hard edges (PP, NP and MP) and open bars are sites with soft edges (PM, NM and MD). Negative distances indicate metres from the edge into the grassland. Reported values are means ± 1 SE.

DISCUSSION

Edge effects on plant diversity and forest structure

Vegetation structure and composition did not appear to respond consistently to the microclimate gradients determined by the edge presence. This can be partially attributable to the high heterogeneity recorded within the forest edges owing to the occurrence of different forms of disturbance, such as forest gaps caused by logging of selected trees and browsing by cattle. Similar interactions between edge effects and forest disturbance resulting in high variability in forest structure and composition have been reported in other tropical systems in Veracruz, Mexico (Williams-Linera 1993; Williams-Linera *et al.* 1998) and Central Amazonia (Kapos *et al.* 1997). Increased disturbance near an edge may increase the edge width and result in edge effects becoming more diffuse. For example Fox *et al.* (1997) found that Australian rainforest fragments with minor disturbance had an abrupt increase in the abundance of forest interior species with increasing distance from the edge. However, in sites with major disturbance (mainly by cattle) the increase in abundance of core rainforest species was more gradual and the density of pioneer species remained high within the forest as well as at the edge.

Forest fragments in the current study area were disturbed by agricultural clearings, logging, fuelwood gathering, or gaps caused by windthrows, becoming virtually all edge habitat. The small forest patch sizes and the occurrence of disturbance within the patches hinder isolation of the effects caused by one edge from influences of nearby edges of different types. According to the "additive edge model", the magnitude of edge effects at any point is equivalent to the sum of edge effects originating from all nearby edges (Malcolm 1994), however this model becomes more complicated if factors such as adjacent land use, edge structure, forest use history, gap dynamics and species specific responses to disturbance are interacting in determining the magnitude and direction of the edge effects.

At small temporal scales, seeds and seedlings are the most vulnerable life stage affected by disturbance (Sousa 1984). In this study, the distribution of seedlings and saplings did not vary with distance from the edge, or with the degree of canopy openness. Similar results have been reported in other studies (Turton & Freiburger 1997; Oosterhoorn & Kappelle 2000; Gehlhausen *et al.* 2000). Restrepo & Vargas (1999) found in a Colombian neotropical montane forest that the distribution of seedlings did not differ between anthropogenic edges and tree fall gaps. In the current research, only the site MP showed an increase in tree seedling density (mainly *Rapanea juerguensenii* seedlings) in the edge. The higher density of seedlings of this species recorded in the edge may be attributable to increased lateral exposure and diffuse irradiance produced by the edge presence. In contrast, in the site NP with an open edge, the lower seedling and sapling densities recorded may be attributed to the relatively high activity of farmers and their animals (cattle and sheep) in the forest interior living near the agricultural clearings as has been reported in other densely populated tropical areas (Oosterhoorn & Kappelle 2000). In all the study sites, the patterns of seedling and sapling distribution can be attributable to the interaction of a) browsing by cattle and sheep, b) disturbance of the forest floor by chickens, c) the distribution of fruiting individuals and seed banks and d) differences in germination resulting from the microclimatic gradients influenced by forest edges, treefall gaps and other forms of disturbance. The relative importance of these factors is not known and probably changes through time and space.

Although overall species composition and the distribution of species belonging to different functional groups did not differ between the edge and the forest interior, differences in the relative importance of individual species between the edge and the forest interior were recorded (e.g. a higher importance value of *Verbesina perymenoides* in the edge), as reported in other studies (Fox *et al.* 1997). This may indicate that several species are suppressed by the shaded forest interior conditions, but they persist, while the edge environment provides appropriate light conditions to enable these species to become more abundant. For example, *R. jueguensenii* seedlings were present along the entire grassland-edge-forest gradient, but were dominant only in the edge of the grasslands (0 to 10 m into the grassland, RIV=

73.5%). This finding supports the need for further species-specific analysis to detect species responses to the edge conditions. Ramírez-Marcial (unpublished) in a study in the Highlands of Chiapas (seven forest fragments in three different localities) found that edge effects on the seedling abundance was highly species-specific, however the same individual species displayed different patterns of abundance in each locality, probably related to differences in forest fragment size.

Edge effects on forest composition

The hypothesis that the edge enhances the presence of early successional species was not supported by the results of this study. The classification of the species used in this study was based on several surveys in different successional habitats in the study area (Ramírez-Marcial *et al.* 1998), however, on-going shade-house experiments (Ramírez-Marcial, unpublished) suggest that there are few different responses between the functional groups (species grouped as in this study) to the light treatments as was originally hypothesised. This result suggests that the presence of some species in different successional stages in the study region might mainly be determined by the availability of propagules (as animal-dispersed seeds) and to a minor extent by the shade intolerance of the species (Hubbell *et al.* 1999). For example, Ramírez-Marcial *et al.* (1996) found that there was a higher frequency of seedlings of *Quercus* spp. under shrubs of *Bacharis vaccinoides*, and on this basis classified them as intermediate species because their abundance and performance is higher under a shrub canopy. However this pattern of abundance could be the result of the higher activity of small mammals leading to a higher probability of acorn dispersal under the shrubs (Callaway 1992). In Chapter 6, it is documented that transplanted seedlings of oaks can grow and survive in open grasslands, therefore oaks may be considered as early successional species (Quintana-Ascencio *et al.* 1992). This supports the need to reclassify the species according to their light requirements (shade tolerant and shade intolerant), determined experimentally, not only based in their appearance in the successional stages. Gehlhausen *et al.* (2000) found that edges are the refuge for saplings of shade intolerant species such as *Quercus* spp., *Carya* spp., *Fraxinus* spp. and *Prunus* spp, and he suggested that

seedlings of these species were unable to compete with shade tolerant species in the forest interior, however Herlin & Fry (2000) suggested that the occurrence in the edge of species such as *Prunus spinosa, Quercus robur, Rosa spp*. and *Sambucus nigra,* may be attributable to the favourable environment that attracts animals or facilitates dispersal of plants towards the edge. The relative importance of seed dispersal and light environment in determining the relative abundance of tree species in the Mexican forests described here remains to be elucidated.

The edge environment appears to provide a favourable microhabitat for several species characteristic of the forest interior, however the results of this study showed that some shade tolerant species that were present in the forest interior were not present in the edge (see Appendix 1: Tables A.1.1-A.1.2). These species have been reported in other studies in the study area as rare or more vulnerable owing to the disturbance regime and special attention should be given to the condition of their populations if they are to be effectively conserved.

In the study area, some relatively shade intolerant species (*Fuchsia encliandra, Arbutus xalapensis, Alnus acuminata*) that occurred in forest edges were also found to be abundant in forest gaps (Mendez-Dewar pers.com.). Gysel (1951) and Wales (1972) compared treefall gap environments and forest edges and found that many of the shade-intolerant species at the edge also occurred within treefall gaps. Gaps in the study area, varying in size and shape, are found in both the centre of the forest patches and near the edges. The differences in the light environments between the central portions of gaps and the surrounding forest matrix are generally not abrupt (Mendez-Dewar pers.com.). The relative importance of edges and gaps in determining the abundance of species in this forest is unknown; it is necessary to investigate under which circumstances edge effects are exacerbated or ameliorated by the influence of forest gaps.

Forest edges may have an influence on canopy gap colonisation within the forest interior by acting as seed sources for shade-intolerant species (Kupfer & Runkle 2003). It has been documented that edges can alter the composition within forest

gaps, with gaps situated closer to the edge exhibiting markedly different composition than gaps located deeper in the forest interior (Goldblum & Beatty 1999; Kupfer & Runkle 2003). This suggests that there is a higher amount of forest affected by the edge than the area predicted by core-area models (Laurance 1991), which do not consider edge-mediated effects.

Edge development

In this study all the clearings investigated had mature edges created more than 30 years ago. It has been suggested that the effects of edges on environmental gradients and plant variables disappear or become more complex as edges age (Matlack 1994). This has been explained by the increase in susceptibility to gap creation near the edge that may occur after the edge has been created (Kapos *et al.* 1997). However, Williams-Linera (1990b) and Turton & Freiburger (1997) documented that canopy openness decreased and became more uniform as the age of the forest edge increased. Old, mature edges tend to be closed off or sealed by vegetation, whereas recently exposed edges may experience more extreme edge effects that penetrate further into the forest (Turton & Freiburger 1997). In contrast, other studies have documented that older edges present more pronounced edge effects. It has been suggested that the edge effects of larger and older clearings are likely to be greater than those resulting from relatively recent tree fall gaps or agricultural clearings, because edge effects will persist longer and affect several stages of the plant cycle (Restrepo & Vargas 1999; Goldblum & Beatty 1999). Given these contrasting results, it seems that the magnitude of edge-induced effects as edges age is determined by the responses of tree species to changes in adjacent land use or disuse that determine edge creation and structure, together with the disturbance regime within the forest (i.e. treefall gaps), as reported here.

Results of this investigation suggested that the age of the edge does not solely account for current edge characteristics because edges were not completely abandoned after creation. Progressive edge development has been linked to forest edge age when edges are abandoned (Matlack 1994; Gascon *et al.* 2000). The land

use history of the studied sites (except NP) suggests that the different periods of abandonment and use produce a cycle of imposition and relaxation of the edge effects as the edge ages. These cycles may explain the similar sapling densities recorded in the edge (0-10 m into the forest) as 10 m into the grassland and the observed patterns in some sites (MP and PP) where scattered isolated saplings (> 1 m tall) mainly of *Quercus* spp, *Pinus* spp., *Rapanea juerguensenni, Ternstroemia lineata* and *Verbesina perymenoides* were present in heavily grazed herbaceous grassland vegetation.

The evenness of the forest/grassland edge in the study area could potentially be predicted with information of the process of secondary succession and the pattern of adjacent land use or disuse. If a clearing is abandoned after the "Milpa', regeneration will be more rapid and the vegetation colonising the clearing will be more diverse (illustrated by the site MD with a well developed shrub stratum) than when the abandoned "Milpa" is used as grassland for several years and then abandoned (Montes-Avelar 2001). The successional pathways after the "Milpa" cultivation have been described previously in the Highlands of Chiapas (González-Espinosa *et al.* 1991; González-Espinosa *et al.* 1995; Ramírez-Marcial *et al.* 1998). Montes-Avelar (2001) found higher species diversity in clearings derived from agriculture in different successional stages (recently abandoned "Milpa", grasslands or shrublands) when these clearings were bordered by forest compared to other habitats. The edge can be considered a source of propagules for forest succession (Ranney *et al.* 1981), by presenting a diverse seed bank (Ramírez-Marcial *et al.* 1992), higher seed production (Restrepo *et al.* 1999) and higher activity of seed predators and/or dispersers (Horvath *et al.* 2001); the larger trees present in the edge may also produce resprouts near the edge (Ranney *et al.* 1981).

Edge sharpness and its implications

Edges vary in their width, length and their vertical structure (Fry & Sarlov-Herlin 1997). In this study the light environment at the soil surface was markedly different between the sites resulting in two types of edges. Three sites (NP, PP and MP) had

edges that were maintained in their original position only by continuing use as permanent grassland of the adjacent field. This edge maintained in the original position may be thought of as a stabilised edge. In contrast, the other sites (PM, MD and NM) presented an abandoned edge that allowed closed herbaceous strata to develop with taller herbs and shrubs near the edge, reducing the potential for edge effects to occur within the forest. In this situation, the edge can be considered as an unstabilised edge because both the original position of the edge and its microclimate have gradually changed over time. Although none of the vegetation variables assessed here characterised the intensity of the adjacent land use, light availability estimated at the soil surface would seem to be the simplest variable that reflects the abruptness of the edge. I draw a simple, but important, message from these observations: although plant communities may not necessarily respond to present edge structure, edge types may nevertheless be reflected in differences in the light environment at the soil surface that may affect other organisms such as small mammals and invertebrates, and processes such as seed germination, predation, dispersal and seedling growth.

This research provides the first account of edge characteristics in the montane forests of Chiapas, and only the second study of forest edges in Mexican montane forests (Williams-Linera 1993). Given the complexity of the historical patterns of land use, the results of this research differ substantially from many of the previous investigations of forest edges, which typically were undertaken in areas of relatively undisturbed forest, prior to the creation of the edges (Laurance *et al.* 1998). The current results indicate that edge effects in fragments of neotropical montane forest are complex under low-intensity sustained human disturbance forest mosaics.

The traditional shifting “Milpa” agriculture practised for centuries by Mayan people in the region, promoted a highly dynamic and diverse forest mosaic, where the long fallow periods after cultivation and the small openings of 0.5 to 2 ha within the forest promoted the fast encroachment of secondary vegetation. Moderate frequency and intensity of disturbance in these systems has promoted high species diversity (González-Espinosa *et al.* 2000). However, several studies have indicated that a

change has occurred in recent years towards widespread shorter fallows and larger openings together with a more intensive use of the clearings (used as permanent grasslands after cultivation), and increased harvesting of fuel or timber within the forest patches (Ochoa-Gaona & González-Espinosa 2000). As a result, natural secondary succession in large clearings within the context of the highly disturbed surrounding matrix becomes more limited by the larger distances to the seed sources, affecting especially seeds dispersed short distances (e.g. those dispersed by small mammals). In terms of edge effects, these changes in the landscape use will result in greater penetration of the edge effects and a gradually receding edge. Therefore, it is necessary to preserve a buffering habitat (long fallow periods) surrounding forest fragments to ameliorate negative edge effects (Mesquita *et al.* 1999; Gehlhausen *et al.* 2000) and maintain the traditional use of small clearings (0.5 to 1 ha) embedded in the forest matrix to enhance secondary succession.

Habitats as edges exist in relation to other habitats within a hierarchy of spatial scales (Donovan *et al.* 1997). Results of this study indicate that at the spatial scale considered, edge effects on plant communities are not evident. However, factors not investigated in this work may be influencing the edge effects on vegetation in the Highlands of Chiapas**.** It is clear from this research that it is necessary to include other forms of forest disturbance (such as position, size and shape of treefall gaps, disturbance by cattle, etc.), a multiscale analysis and multivariate techniques are recommended to include several forest edges with different ages, adjacent land uses or structures, and forest disturbance regimes. Additionally landscape variables, such as forest size, shape, position in the matrix, connectivity and edge area, should be considered (Donovan *et al.* 1997; Ochoa-Gaona & González-Espinosa 2000; Ochoa-Gaona 2001). Instead of emphasising depth or presence of edge effects and the edge-related patterns on plant communities, as in previous research, future studies in forest mosaics should examine the dynamic influences that edges may have on processes (Wiens *et al.* 1993; Murcia 1995) within forest remnants, adjacent areas and across the landscape (i.e. edges as dispersal barriers or filters).

CHAPTER 3: Permeability of forest edges: consequences for oak dispersal.

ABSTRACT

The permeability of habitat edges and its consequences for oak dispersal were investigated in a forest mosaic in the Highlands of Chiapas, Mexico. During two consecutive years, edge type (hard and soft) and distance from the edge, both into forest patches and into neighbouring grasslands, were related to acorn production, acorn removal and dispersal, and the abundance and composition of small mammal communities. During the non-mast seeding year acorn removal was faster than in the mast-seeding year (85% removal within 138 days vs. 75% within 213 days). The results indicated that edge type affects whether or not acorn removal is affected by distance from the edge (Logistic regression models, $P<0.05$). There was a decrease in acorn removal in grasslands in sites with hard edges. Movements of metal-tagged acorns support the hypothesis that soft edges are permeable to small mammals, and rodents move acorns up to 15 m into the grasslands in soft edges. In hard edges, higher rates of acorn dispersal and removal were recorded within the forest edge and forest interior. *Peromyscus* species were the main acorn predators and/or dispersers of acorns. The rate of acorn removal varied between years, demonstrating that in mast seeding years some seeds may escape predation by animals. The implications of these results for oak dispersal and regeneration in fragmented forest landscapes are discussed.

INTRODUCTION

Forest mosaics created through small-scale clear cutting and localised logging contain neighbouring patches of different vegetation types. The characteristics of edges separating elements in a landscape can have important influences on the ecological processes within homogeneous patches and between components of a landscape (Wiens *et al.* 1985). Most vectors as organisms, material and energy moving between different patches must pass through the edge. Vectors may impose

non-random, directional fluxes of materials, from one patch to another (Wiens *et al.* 1985). How edges mediate these fluxes is determined by the edge permeability (Cadenasso & Pickett 2000). An edge may be a complete barrier or act as a simple semi-permeable membrane: for example, forest edges can be permeable to habitat generalist species but can halt forest specialists (Laurence *et al.* 2001). Permeability measures the tendency of an edge to inhibit or enhance movement of organisms across it, and is determined, among other factors, by the concentration of material or species in adjacent patches (Lidicker 1999; Sarlov-Herlin 2001) and the relative proportions of elements enhancing or restricting movement (Wiens 1995; Lidicker 1999).

Edge permeability has been included in edge effects models (Stamps *et al.* 1987) and studied for different fluxes of a) benthic invertebrates into seagrass (Holmquist 1998), b) exotic weeds into forest (Honnay *et al.* 2002), c) herbivores into forest (Cadenasso & Pickett 2000), d) arthropods into cultivated areas (Duelli *et al.* 1990) and e) seeds into forest (Cadenasso & Pickett 2001). These fluxes were studied as a function of edge structure or edge types. Patches within fragmented landscapes may be bounded by what can be termed 'hard edges', which comprise an impermeable boundary that organisms never cross in order to enter surrounding habitats (Stamps *et al.* 1987). On the other hand, patches may be bounded by 'soft edges' that are permeable to emigrating organisms and other fluxes (Stamps *et al.* 1987). A main concern in the context of biodiversity conservation is how the fluxes directed into a forest fragment may influence forest dynamics (Cadenasso & Pickett 2000; Cadenasso & Pickett 2001; Honnay *et al.* 2002; Kollmann & Buschor 2002). In addition, fluxes from a forest fragment into open or disturbed sites may have a major influence on plant dispersal and forest expansion (Ostfeld *et al.* 1997; Manson & Stiles 1998; Hubbard & McPherson 1999; Meiners *et al.* 2002) and therefore have major implications for conservation approaches at the landscape scale.

Studies of edge-related effects on small mammals (see review in Lidicker 1999) have reported an increase in species diversity (Pasitschniak-Arts & Messier 1998; Stevens & Husband 1998; Horvath *et al.* 2001) and abundance (Manson *et al.* 1999)

together with behavioural changes associated with the presence of edges (Anderson & Boutin 2002). The abundance of individuals may increase near the edge (a positive ecotonal effect (Manson & Stiles 1998; Lidicker 1999) as has been reported for a) *Sorex cinereus* and *Clethrionomys gapperi* (Menzel *et al.* 1999), b) *Peromyscus maniculatus* (Bayne & Hobson 1998), c) *Microtus pennsylvanicus* (Pasitschniak-Arts & Messier 1998) and d) *Melomys cervinipes* (Harrington *et al.* 2001). Some small mammal species that are habitat specialists may avoid the edge and their abundance may decrease near the edge (a negative ecotonal effect) as has been reported for a) *Microtus pennsylvanicus* (Manson *et al.* 1999), b) *Metachirus nudicaudatus* (Stevens & Husband 1998), c) *Peromyscus maniculatus* (Kristan III *et al.* 2003) and d) *Clethrionomys californicus* (Mills 1995). The abundance of some species may also decline sharply from species-rich to species-poor habitat: the so-called matrix effect (Lidicker 1999) or habitat effect (Kingston & Morris 2000). In this case, the abundance reflects the relative qualities of the two adjacent habitats but there is no edge effect (Lidicker 1999; Kingston & Morris 2000). This pattern has been reported for *Peromyscus leucopus, Ochrotomys nuttalli, Microtus pinetorum* among other species (Heske 1995; Stevens & Husband 1998). Other small mammal species (habitat generalists) have shown no edge recognition and move easily across two adjacent habitats (Bayne & Hobson 1998; Menzel *et al.* 1999).

The contrasting results obtained by previous studies may reflect the fact that the same edge may evoke different effects with different species (Lidicker 1999; Menzel *et al.* 1999), and the same species (e.g. *Peromyscus* spp.*, Clethrionomys gapperi*) may present different edge-related responses in different edge types (Kingston & Morris 2000). Edge effects on small mammals are not only species-specific, but also sex- and age-specific (Lidicker & Peterson 1999).

Growing evidence suggests that a dynamic interaction exists between small mammals and plant communities (Manson & Stiles 1998; Manson *et al.* 1998; Brewer & Rejmánek 1999; Manson *et al.* 1999). Considering the variation recorded in the edge-related responses of small mammals, it is not surprising that observations of edge-related seed predation patterns by small mammals are similarly variable. For

example, some studies have reported lower seed removal rates near the forest edge (Bowers & Dooley 1993; Burkey 1993; Manson & Stiles 1998; Restrepo & Vargas 1999; Diaz *et al.* 1999). Other studies have documented higher seed removal near the edge (Bonfil & Soberon 1999; Kollmann & Buschor 2002; Jones *et al.* 2003; Jules & Rathcke 2003) whereas still others found no difference in seed removal between the edge and forest interior or other habitats (Myster & Pickett 1993; Notman *et al.* 1996). Most of these results are species-specific (Holl & Lulow 1997; Manson & Stiles 1998) or edge-type specific (Kollmann & Buschor 2002) and show spatial variance (Bowers & Dooley 1993). Thus, new experiments are needed in order to differentiate between site- or species-specific responses and more general mechanisms of edge effects on seed removal. Such studies should identify the seed predators and/or dispersers and analyse the edge vegetation structure that is related to small mammal preferences (Kollmann & Buschor 2002).

The montane forests of Mexico provide an outstanding opportunity to study the effects of habitat edges on the processes of seed dispersal and predation by small mammals. The forests of central and southern Mexico are probably the richest areas (60-75 species) of *Quercus* (oak) diversity in the Western Hemisphere (Nixon 1993). Small mammals play an important role both as predators and/or dispersers of acorns in these forests (Quintana-Ascencio *et al.* 1992) as in many other forests where oaks are dominant (Watt 1919; Shaw 1968; Price & Jenkins 1986; Briggs & Smith 1989; Quintana-Ascencio *et al.* 1992; Steele & Smallwood 2002). However, very little is known about the edge-related movements of acorn predators and their importance as acorn dispersers into open habitats (Jensen & Nielsen 1986; Hubbard & McPherson 1999). Edge-mediated effects of the fluxes (into the forest and into the open patches) of acorn predators and the net effect on acorn survival has never previously been assessed in a single investigation.

In oaks, seed production varies considerably from year to year, mast years occurring at 2-6 year intervals (Sork 1993; Sork *et al.* 1993). It is well documented that episodic production of acorns (masting or mast seeding years) is related to fluctuations in populations of small mammals such as *P. leoucopus, P. maniculatus*

and *Tamias striatus* (Ostfeld *et al.* 1996; Wolff 1996; Schnurr *et al.* 2002). Mast seeding produces a large pulse of food resources and as a result populations of seed predators and/or dispersers increase the following year (Wolff 1996; Curran & Leighton 2000; Schnurr *et al.* 2002; Margaletic *et al.* 2002). In inter-mast seeding years, decreased acorn production is unable to sustain high seed predator populations, thus the abundance of seed predators is low during the following mast (McShea 2000), increasing the probability of predation satiation, when food production exceeds the number of seeds that can be consumed by the total predator complex (Janzen 1971b). The impact of annual variation in seed production on patterns of acorn predation and dispersal, in relation to the effects of habitat edges, has not previously been investigated.

The aim of the present investigation was to examine edge permeability as a function of different habitat edge types, and its role in influencing patterns of acorn removal and dispersal by small mammals. The overall hypothesis of this study is that as structural similarity between two adjacent habitats increases, the edge created between the habitats will become less abrupt, and the likelihood of movement of small mammals between the habitats will increase (Laurence *et al.* 2001). To test this hypothesis I assessed the flux of acorns moved by small mammals across forest edges. Hard and soft edges were compared because they provide a clear contrast of how vegetation structure may affect edge permeability.

I hypothesised 1) that within the forest interior, acorn removal is positively associated with distance from the forest edge, but this relation is only present in habitat patches with abrupt or hard edges; 2) soft edges are associated with higher edge permeability, which will be reflected in higher acorn removal and dispersal in grasslands adjacent to forest patches with soft edges than with hard edges; 3) according to the satiation model, which predicts that when acorn production increases probability of seed predation decreases, in mast years acorn survival will be higher.

METHODS

Experimental plots

A detailed description of the study area is available in Chapter 2. Two edge types were recognised in the studied forest mosaic. Hard forest edges are those where adjacent vegetation has a simple homogeneous structure, such as that observed under intensive agriculture, thus creating a sharp contrast with adjacent forest cover. Conversely, soft edges are created by a matrix of more structurally complex successional vegetation maintained for several metres (15-20 m) from forest edges or arising from agricultural abandonment. Sites with soft edges are characterised by dense vegetation (shrubs, tree saplings and tall herbs) that gradually declines in height between the edge and the grassland. For the purposes of this study, six sites with grasslands and adjacent pine-oak forest (three sites with hard edges and three sites with soft edges) were chosen (details of the experimental plots are presented in Chapter 2).

The forest of the six sites was characterised by measuring the vegetation structure, composition and the incidence of human disturbance. Herbaceous and shrub composition was also studied (see details in Chapters 2 and 6). The sites selected were named after their owner's name initials. Soft edges were PM, NM and MD. Hard edges were PP, NP and MP. A rectangular experimental plot (20 x 60 m) was established (25 m from the edge into the grassland and 35 m into the forest) in each selected site and was fenced with a 2-m high steel wire mesh (mesh size of 4.5 cm) to exclude livestock. The selection of the experimental plot position was based on a) the edge sharpness and b) the side of the opening that had a larger continuous forest fragment. When necessary, grasslands within the fenced areas in sites with hard edges were maintained by removal of vegetation (maintaining the herbaceous stratum height at 5 to 10 cm in order to mimic their original grazing pressure) at regular intervals (every 6 weeks) but more frequently during the rainy season. Mean distance between study sites was 588 ± 276 m (± SD).

Acorn crops

During two consecutive years, acorn production was estimated. At least five fruiting oak trees were selected by using the nearest tree method (every 20 m) on transects situated at the forest edge, 20, 40 and 60 m running parallel to the edge. Fruiting individuals were tagged and characterised by their species, dbh, and distance to the edge. Acorn production per tree was estimated by sampling four 1 x 1 m quadrats (located 1.5 m from the trunk at the four cardinal points) on the forest floor during the acorn fall. This estimate of acorn abundance is conservative since it does not consider the number of acorns removed by predators/and or dispersers such as birds, squirrels and small rodent species either from the canopy before they fall to the ground, or from the ground prior to the assessment.

The following acorn types were identified from the samples: a) mature, b) mature with cups, c) immature, d) germinating, e) aborted, f) attacked by weevils (*Curculio* sp.), g) damaged by birds, h) damaged by small mammals and i) produced the previous year. For the estimation of total acorn production, aborted acorns, cups and past year production were not included in the analysis.

Small mammal trapping

A capture-mark-recapture study of the small mammal populations in each experimental plot was carried out concurrently with the acorn removal experiments. This trapping protocol immediately preceded or followed the acorn removal experiments. Twenty-seven traps were distributed in grids (9 by 3 array) with 10 m spacing between. Grids crossed the edge and extended 50 m into the forest and 30 m into the grassland. Medium Sherman live traps (5.1 x 6.4 x 15.2 cm) were baited with oatmeal and vanilla. Trapping in each experimental plot was set for three consecutive days each two months with traps checked in the morning and reset in the late afternoon. Each animal captured was marked with a uniquely numbered ear tag. Ear tag number, species, gender, reproductive condition and body mass were recorded. After recording data, each animal was released at point of capture. A total of 2916 trap nights (36 nights x 81 traps) were accumulated.

Observations of acorn predators and/or dispersers

The activity of jays, pigeons and woodpeckers was observed during the acorn production periods for two years. Squirrels were observed during the second year. All these animals were observed eating acorns in oak trees, picking them from the branches or cutting them loose with their teeth. The relative abundance of birds and squirrels was estimated using point census counts. Censuses were conducted at two points (grassland and forest) in each experimental plot, stopping 15 minutes at each point. The observations were made with binoculars (10 x 50 Bushnell Inc. Lexena, USA) over three consecutive days. Detection of animals during point counts was influenced by many factors such as behaviour of species, vegetation characteristics and presence of occasional mist. Some difficulties were encountered in detecting squirrels because these animals are intensively hunted in this region and they avoid human presence.

Post-dispersal removal trials

A pilot study of removal of *Q. candicans* acorns was performed during July 2000 (see Appendix 2).

Species

Quercus laurina (subgenus *Erithrobalanus*) is an evergreen tree (10-40 m tall) and produces acorns during autumn. Acorns usually display dormancy and germinate during the first winter rains (December-January in the study area). Like most oaks, it does not form a persistent seed bank in the soil. During September 2000 and November 2001 *Q. laurina* acorns were collected from at least 30 trees and tested by floating them in water, which is a reliable method to identify damaged acorns (Gribko & Jones 1995); only those which sank in water were exposed to seed predators. Acorns of approximately the same size were chosen for each removal trial (fresh mass 1.80 ± 0.64 g, ± SD, diameter 1.34 ± 0.17 cm, n=100). All the

experiments were undertaken at the time of the year when the natural dispersal of this species occurs.

I tested if removal rates of *Q. laurina* acorns varied in relation to exclosure, distance from edge, edge type (hard vs. soft edge) and year (1 vs. 2). The experiments were performed during two consecutive years. Acorns were introduced in January 2001 and January 2002. To evaluate the relative contribution on acorn predation/dispersal of small mammals, and other acorn consumers, the following selective treatments were used: 1) small mammal enclosure: 4-5 cm wire mesh cages (30 x 30 x 30 cm), leaving acorns available to small rodents or insects but not birds or squirrels and 2) open treatment: no exclusion methods were used, acorns were available for all predator types.

At each study site 20 m transects were established at different distances (-20, -10, 0, 10, 20 and 30 m) parallel to the edge in each of two adjacent habitats. Each enclosure treatment was replicated twice in each distance. Two paired squares were marked on the ground with a pile of acorns in the centre. These paired squares were replicated along the transect with 18 m spacing between them (Fig. 3.1).

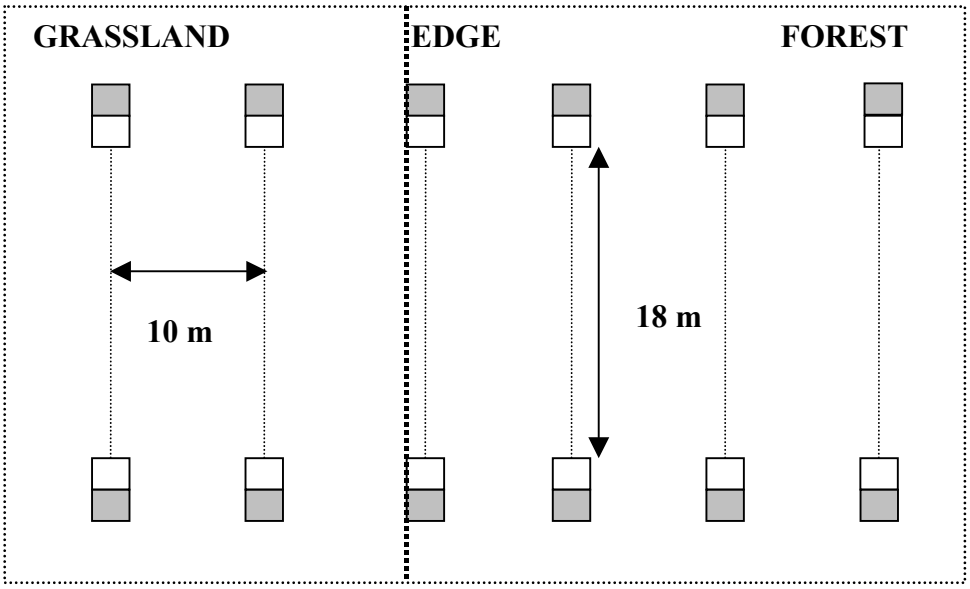

Fig. 3.1 Diagram of the experimental design. Each quadrat represents the two exclusion treatments (caged and uncaged). The same protocol was used in each of the six sites: three sites with hard edges and three sites with soft edges.

Acorns were placed in each square in piles of 10 acorns. Transects were censused every three days for the first two weeks and weekly thereafter until all acorns were gone or had germinated. Seed fate was scored by placing each acorn into one of the following categories: remaining (whole), opened or crushed, germinated, with insect damage or removed. Final fate of removed acorns is uncertain, for that reason the term predation will not be used in these experiments.

Microhabitat characteristics

Microhabitat characteristics were measured in each square (in the same square where the predation trials were positioned) in each experimental plot. Percent cover of grasses, seedlings and woody shrubs was measured using the line (1 m long) intercept method (Mueller-Dombois & Ellenberg 1974). Percentage of bare ground, leaf litter cover and dead wood cover were also recorded. Along this line, forest floor depth and height of herbaceous stratum was measured every 10 cm. Percentage of shrub cover at 0.50-1.0 m and canopy cover at 1-2 m were also recorded along the 1 m line. Total vegetation cover was estimated with a spherical densiometer (Forestry Suppliers Inc. Battlesville, Oklahoma, USA), and light reaching the soil surface (PAR μmol m^{-2} s^{-1}) was quantified with a ceptometer (Quantum sensor, Decagon, Pullman Washington, USA).

Acorn dispersal

To assess acorn dispersal, acorns were tagged so that their fates could be followed when they were removed. The acorns were drilled with a hand drill and a small nail (15 by 3 mm) was inserted inside each acorn (Sork 1984). The head of the nail in each acorn was exposed above the surface and painted with fluorescent spray paint to facilitate their relocation in leaf litter and also to differentiate oak species. Metal-tagged acorns were placed on the forest floor at the forest edge and exposed to predators. A metal detector (Discriminator metal detector Very low frequency, Radio Shack /Tandy corporation, No. 63-3006) was used to search tagged acorns.

During April 2002 a pilot experiment to see whether tagged acorns would be removed as readily as untreated acorns was conducted. I also tested whether the painted nails had an effect compared with the unpainted nails and whether the different age of the acorns had an effect on the probability of removal. This study was set out in the study areas to avoid problems of mammals foraging habituation and contamination of nails. A forest edge with adjacent grassland was selected. Paired clumps of 25 acorns were placed within enclosure cages (4-5 cm wire mesh; 30 x 30 x 30 cm) along the forest edge. The following combinations were tested: 1) nail painted tagged acorns vs. untreated acorns, 2) unpainted nail tagged acorns vs. untreated acorns, 3) 1 year (old) vs. 4 months acorns (new), 4) new tagged acorns vs. new untreated acorns and 5) old tagged acorns vs. old untreated acorns. Two replicates of each treatment combination were set up. Within a month all acorns had disappeared regardless of the acorn condition. These results indicate that the tagging method and the acorn age do not affect the probability of acorn removal by small mammals. The effect of this method on the seed germination in the laboratory was also evaluated. Germination of tagged *Q. laurina* acorns (89.3 ± 5.3%, ±1 SE) and intact acorns (78.7 ± 10.9%) was not different (F=0.16; df=1, 2; P=0.729).

In two study sites, PM and PP, one soft edge and one hard edge, acorns of *Quercus candicans* (4 month old) and *Quercus laurina* (one year old) were introduced during May 2002. Exclosure cages (4-5 cm wire mesh; 30 x 30 x 30 cm) stapled at each corner to a metal stake about 5 cm from the ground were used to exclude birds and squirrels from this experiment. Two different clumps of acorns were placed within the cages on the forest floor at the edge: 1) a clump of 1250 *Q. candicans* tagged acorns, 2) a mixed clump with 390 *Q. laurina* acorns and 390 *Q. candicans* acorns. Nails introduced in *Q. laurina* and *Q. candicans* acorns were painted with different colours. A total of 4060 tagged acorns were introduced.

Each cage was positioned evenly along the forest edge with 5 m between each. After 15 days, removed acorns were counted and tagged acorns were relocated. Careful searches (forest floor, under logs, under very low branches, holes in trees, etc.) were made within the fenced plot (20 m into the forest and 20 m into the grassland: 40 x

20 m). In both areas a total of 1600 m^2 was searched. If the nail was relocated with the seed still attached and it had been moved, secondary dispersal was indicated. If the nail alone was recovered, the seed had been predated. For each recovered nail (or tagged acorn), acorn condition (whole, partially eaten, embryo excision, etc) was registered. The surrounding microenvironment of the relocated-tagged acorns was estimated by measuring litter depth and a visual estimation of percentage of shrub and herbaceous cover. The distance of the tagged seeds, tags or fragments to their original release points was measured. The exact location of all nails and cached acorns were marked with a numbered flag.

Statistical analysis

Estimated acorn abundance (number of acorns per tree) was transformed ($\log_{10}$ + 0.25) and analysed with General Linear Models. Proportions of germinating, insect damaged and mammal damaged acorns were transformed (arcsine of the square root). The effect of year (1 and 2), edge type (hard and soft), distance from the edge (0, 20, 40, and 60 m) and their interactions were tested in both analyses (General Linear Model procedure, SPSS v.10.0.1). All full ANOVA tables are presented in Appendix 2 (Tables A.2.1-A.2.6) in the same order as they were reported in the results section.

For the small mammals capture-recapture protocol, mean abundance was expressed as the total number of captured animals (2916 trap nights). Differences in the distribution and abundance of *Peromyscus* species and the other species were examined using contingency tables and Chi-squared tests of homogeneity. The number of animals trapped was analysed as a function of edge type and distance from the edge.

Acorn removal data at the end of the experiments appeared to be bimodal (all or most of the seeds were either present or missing), therefore acorn removal was considered categorical rather than continual. I transformed acorn survival (number of acorns remaining / number of acorns originally placed), into a categorical variable with two

levels (1 = 10 acorns removed, 2 = less than 10 acorns removed). The probability that at least one acorn could be removed from the pile, equivalent to the probability that the clump could be found by any seed predator was also tested as a categorical value (0 or 1).

Because the dependent variables have binary responses a logistic regression analysis was performed. The Logistic procedure was used (SAS v. 8.0, SAS Institute Inc.) to fit linear logistic regression models for ordinal response data by the method of maximum likelihood. The logistic model included the effect of year (1 and 2), edge type (hard and soft) and distance from the edge (-20, -10, 0, 10, 20 and 30 m). All possible interactions were tested. Statistical significance of the effect of the explanatory variables was determined by chi-squared tests of the information matrix from the maximum likelihood calculations.

As a second analysis, temporal patterns of probability of detecting acorn piles over time were compared for the experimental factors: year, edge type and distance from the edge using the Kaplan-Meier method. I used this method instead of Gehan's Wilcoxon test, because the time variables cannot be aggregated into equal time intervals. The Kaplan-Meier model is based on estimating conditional probabilities at each time point when an event occurs and taking the product limit of those probabilities to estimate the survival rate at each point in time (Life tables procedure, SPSS v.10.0.1). Log-rank tests were used to perform pairwise comparisons and test for heterogeneity among levels within the factors (Fox 2000).

Spearman rank correlations were used to explore the relationship between microhabitat variables. Those variables that were highly correlated were excluded. The selected variables canopy openness (%) estimated at the soil surface, height of the herbaceous stratum, proportion of dead wood and shrub cover (0.5 to 1 m) were transformed into categorical variables and included in a multiple binary logistic regression model to predict the acorn removal intensity in each of the edge types (Logistic regression procedure, SPSS v.10.0.1). Negative distances indicate metres

from the edge (0 m) into the grasslands. Throughout the text means are given ± 1 SE unless otherwise stated.

RESULTS

Acorn production

In year 1 (2000/2001), acorn fall occurred in early September, whereas in year 2 (2001/2002), acorn fall was delayed, commencing in November 2001. Acorn production varied markedly between years (F=35.12; df=1, 30; $P < 0.001$). In year 1 a mean density of 161.1 ± 19.4 acorns m^{-2} was recorded under the crowns of the sampled trees, whereas in year 2, mean density was only 21.3 ± 2.9 acorns m^{-2}. The highest mean density of acorns was observed in year 1 within site NM (294.8 ± 75.1 acorns m^{-2}). There were no significant differences in acorn density between edge types and distances from the edge (ANOVA, P>0.05).

Assessments of the sampled acorns showed that the mean percentage of acorns germinating and damaged by insects did not vary between years, edge types or distances from the edge (P>0.05). Mean percentage of acorns exhibiting damage by insects was 10.9 ± 1.5 during year 1 and 13.9 ± 1.9 during year 2. These numbers may be underestimates as weevils may remain inside the acorn without producing damage evident from the exterior. Mean percentage of acorns damaged by small mammals varied between edge types (F= 5.90; df=1, 30; P=0.021); in sites with soft edges, sampled trees had a higher proportion of acorns damaged by small mammals (11.1 ± 1.8%) compared with trees in sites with hard edges (5.1 ± 0.9%). This difference was mainly attributable to sites NM and PM.

Small mammals

A total of 2916 trap nights resulted in 213 captures of 166 individuals from eight species. The overall trapping success was 0.07. Species of small mammals captured in this study were: Southern Brush Mouse (*Peromyscus levipes* Merriam; n=83 individuals), Fulvous Harvest Mouse (*Reithrodontomys fulvescens* J. A. Allen;

n=30), Sumichrast's Harvest Mouse (*Reithrodontomys sumichrasti* Saussure; n=21), Aztec Mouse (*Peromyscus aztecus* Saussure; n=21), Crested-Tailed Mouse (*Habromys lophurus* Osgood; n=2), Mexican Deer Mouse (*Peromyscus mexicanus* Saussure; n=7), Chiapan Deer Mouse (*Peromyscus zarhyncus* Merriam; n=1) and Roof Rat (*Rattus rattus*; n=1). Total number of animal caught showed great seasonal variation; was extremely low during September 2000 (two individuals / 486 trap nights), but increased substantially the following autumn (48 individuals / 486 trap nights), with the maximum abundance recorded in July 2002 (73 individuals / 486 trap nights).

Total frequency of *Peromyscus* animals captured was affected by the interaction between edge type and distance from the edge (χ^2 =26.43; df=8; *P*=0.001), while the other species captured were not significantly affected by this interaction (χ^2 =14.06; df=8; *P*=0.080). *Peromyscus* abundance was most closely related to the forest interior; however, the fact that 17 individuals of *P. levipes,* three of *P. mexicanus* and two of *P. aztecus* were captured in the grassland across the soft edges, suggesting that these species were responsible for most of the acorn removal in these habitats (Fig. 3.2a). Hard edges were almost impermeable to *Peromyscus* animals, as only two individuals of *P. levipes* were found in the grasslands during the summer of 2002 (when resources were scarce after the non-masting year). Before that trapping session, no *Peromyscus* animals were found in the grasslands across sites with hard edges. *Reithrodontomys* animals accounted for 24% of the total captures and were much more common in the grasslands than in the forest interior; however, *Reithrodontomys* together with the rest of the species showed a broader distribution along the forest-edge-grassland gradient regardless of the edge type (Fig. 3.2b).

Peromyscus animals in hard edges concentrated their movements within the forest and within the forest edge (Table 3.1a). One individual of *P. levipes* travelled 50 m from the hard edge into the forest. All of the movements detected by repeated recaptures in sites with hard edges were within the forest or along the edge. In sites with soft edges, seven *Peromyscus* individuals were recorded that travelled between

the forest, edge and grassland, showing how the edge type affected the magnitude and direction in the flux of *Peromyscus* animals (Table 3.1b).

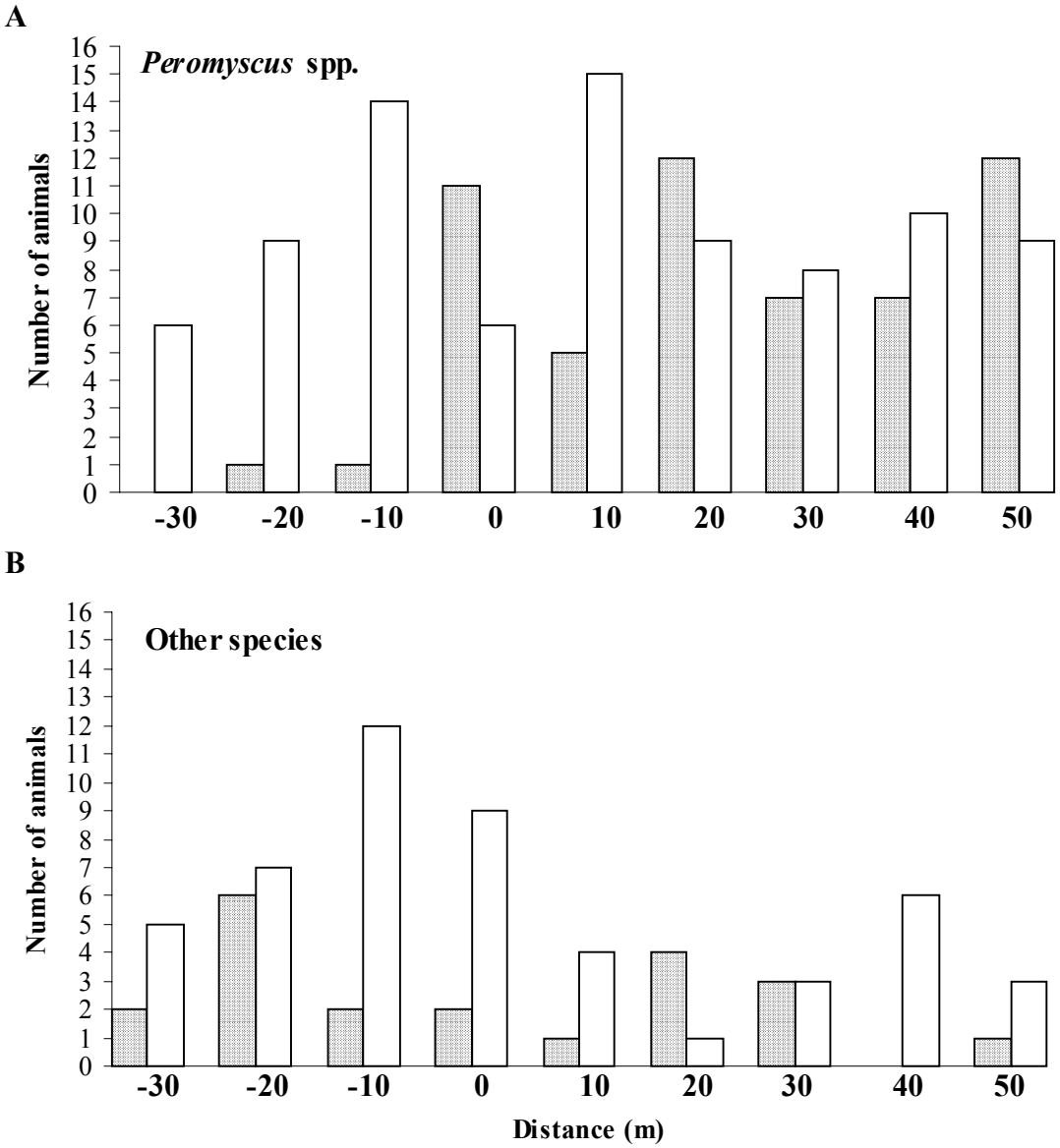

Fig. 3.2 Number of animals captured per 2916 trap nights of a) *Peromyscus* species and b) the rest of the trapped species along the forest-edge-grassland gradients in sites with two different edge types: hard edges (shaded bars) and soft edges (open bars). Negative distances indicate metres from the edge (0 m) into the grasslands.

Table 3.1 Description of the movement patterns of small mammals detected by the capture-recapture study. Numbers in each habitat are the number of animals recaptured and numbers within parentheses are the average movement distances (± SD). A. small mammal movements detected within each habitat and B. small mammal movements detected between habitats.

A

Edge type	Species	Forest	Edge	Grassland
Hard	*Peromyscus* species	6 (16.7±5.2)	2 (5.0±7.1)	
	Other species		1 (0)	
Soft	*Peromyscus* species	5 (12.0±10.9)	1 (10)	1 (10)
	Other species	3 (13.3±5.8)	3 (6.7±5.8)	3 (3.3±5.8)

B

Edge type	Species	Forest	Edge	Grassland
Hard	*Peromyscus* species	←	1 (50)	
Soft	*Peromyscus* species	1(20)	→	
	.	←		3 (40.0±20.0)
			←	3 (13.3±5.8)
	Other species	←	1 (50)	

Other acorn consumers

Bird observations indicated that the main putative predators and / or dispersers of acorns at the study sites were, in declining order of abundance: Band-tailed pigeon (*Columba fasciata fasciata*), Unicolored Jay (*Aphelocoma unicolor*), Hairy Woodpecker (*Picoides villosus*), Northern Flicker (*Colaptes auratus mexicanoides*), Steller's Jay (*Cianocitta sterelli*), Acorn Woodpecker (*Melanerpes formicivorus*), Black-throated Jay (*Cyanolica pumilo*) and Red-billed Pigeon (*Columba flavirostris*). Groups of up to approximately 60 individuals of Band-tailed pigeons were observed foraging in oak trees during the acorn abscission period, usually in one or two trees at each time. The site with the highest number of birds recorded was PM, a soft edge accounting for 25.4% (140/550) of the total number of observations made in both years. Only four individuals of Grey squirrel (*Sciurus aureogaster* Cuvier), and one

individual of Red squirrel (*Sciurus deppei* Peters) were observed during the second year.

Acorn removal

After 213 days of exposure to predators and/or dispersers, overall mean percentage of acorn removal was 74.8 ± 3.4% in year 1, and after 138 days in year 2, acorn removal was 85.1 ± 3.7%, this difference being not significant (χ^2=0.28, df=1, *P*=0.596, Logistic regression). In year 1 at the end of the experiment, of the total number of remaining acorns, 34.5% germinated with only the radicle visible (n=55), 16.1% germinated and produced seedlings (n=57), and 16.9% were intact and apparently viable. The remainder of the acorns (32.5%) exhibited insect damage or fungal infection, or were desiccated. At the end of the experiment in year 2, none of the remaining acorns produced seedlings and only 7.5% (n=16) were germinating. 39.7% (n=85) of the acorns remained viable and the others (52.8%) exhibited damage by insects or fungi, or were desiccated.

Regardless of the year, acorn removal in open treatments was similar to that within exclosure cages (χ^2=2.57; df=1; *P* =0.108), showing that small rodents were the most important consumers of acorns in the studied sites. Therefore values from each treatment were pooled to analyse the effects of the other experimental factors.

As predicted, regardless of the year, there was a significant interaction between edge type and distance from the edge, which affected the intensity of acorn removal (χ^2=4.58; df=1; *P*=0.032, Logistic regression). In sites with hard edges, distance from the edge affected acorn removal, whereas no such effect was found in sites with soft edges. The effect of distance from the edge on acorn removal was exclusively due to the values recorded in the grasslands. There was a decrease in acorn removal in grasslands in sites with hard edges. However, contrary to expectations, no edge effects were recorded within the forest and no emergent properties of the edge were recorded; acorn removal within the forest near hard edges did not vary compared to the forest interior or to soft edges (0 m; Fig. 3.3).

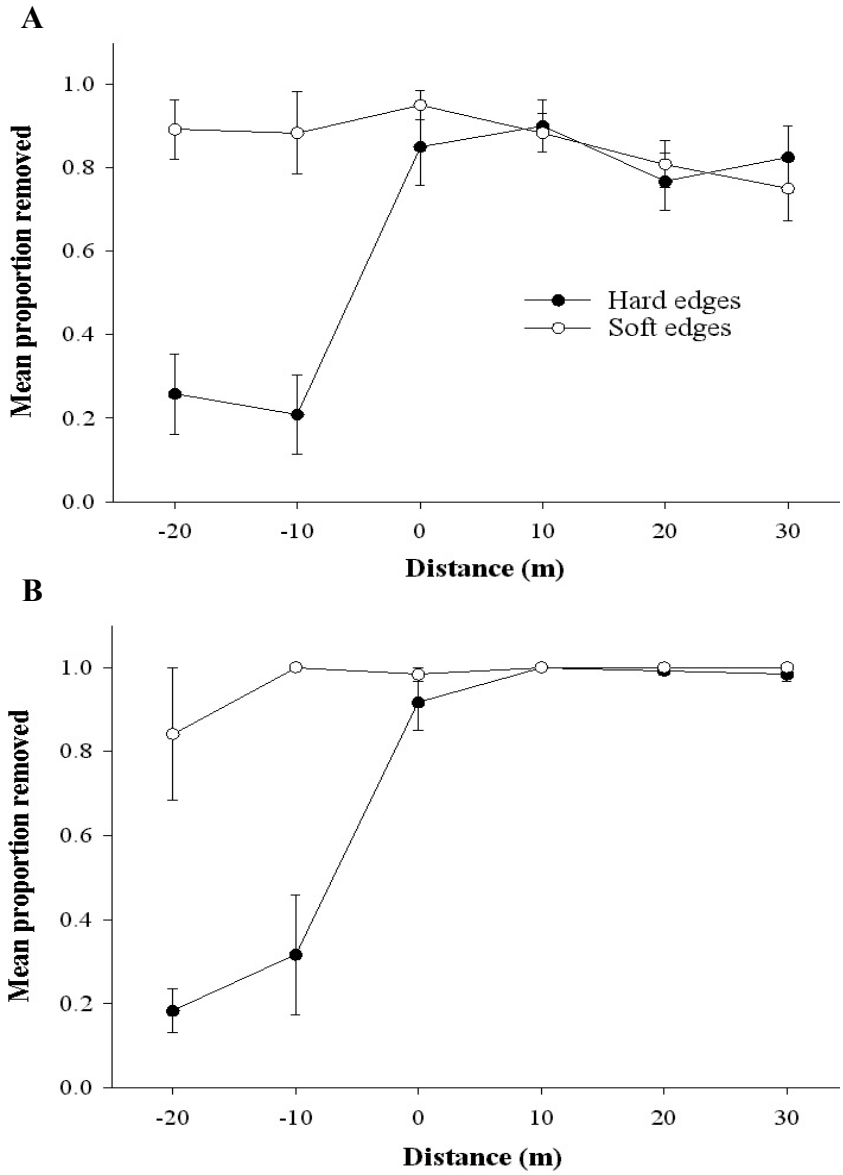

Fig. 3.3 Mean proportion of acorns removed (± 1 SE) at the end of the experiment in A) year 1 (masting year) and B) year 2 (non-masting year), as a function of edge type (hard and soft edges) and distance from the edge. Negative distances indicate metres from the edge (0 m) into the grasslands.

Probability of detecting acorn piles

At the end of the experiments, acorn consumers detected most of the piles of acorns (95.8% year 1 and 97.9% year 2). The final probability of detecting acorn piles was not significantly affected ($P>0.05$ Logistic regression) by any of the experimental factors (years, edge types or distances from the edge).

A significant difference in the rate of detection of the piles was recorded among years (log rank=517.0; df=1; P<0.001). Piles of acorns were detected more rapidly during year 2 (non-masting year) than year 1 (masting year, Fig. 3.4). During year 1, distance from the edge affected the rate of pile detection, but this effect only occurred in sites with hard edges (log rank=92.40; df=5; P<0.001; Fig. 3.5a) and not in those with soft edges (log rank=7.23; df=5; P=0.204; Fig. 3.5b). During year 2, similar results were obtained, with a significant effect of distance in sites with hard edges (log rank=25.56; df=5; P<0.001; Fig. 3.5c) but not in sites with soft edges (log rank=6.54; df=5; P=0.257; Fig. 3.5d). Piles of acorns in sites with hard edges were detected more rapidly within the forest, than within the grasslands (Fig.3.5a and 3.5c).

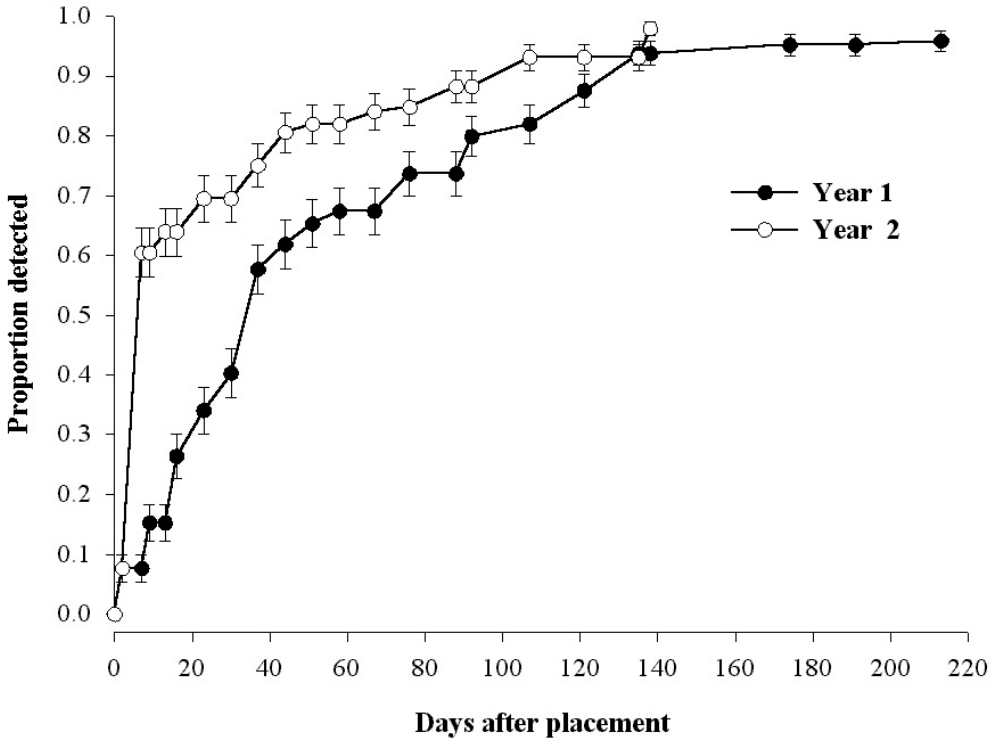

Fig. 3.4 Mean proportion (± 1 SE) of piles of *Q. laurina* acorns detected through time as a function of years. Year 1 was a masting year, and year 2 was a non-masting year.

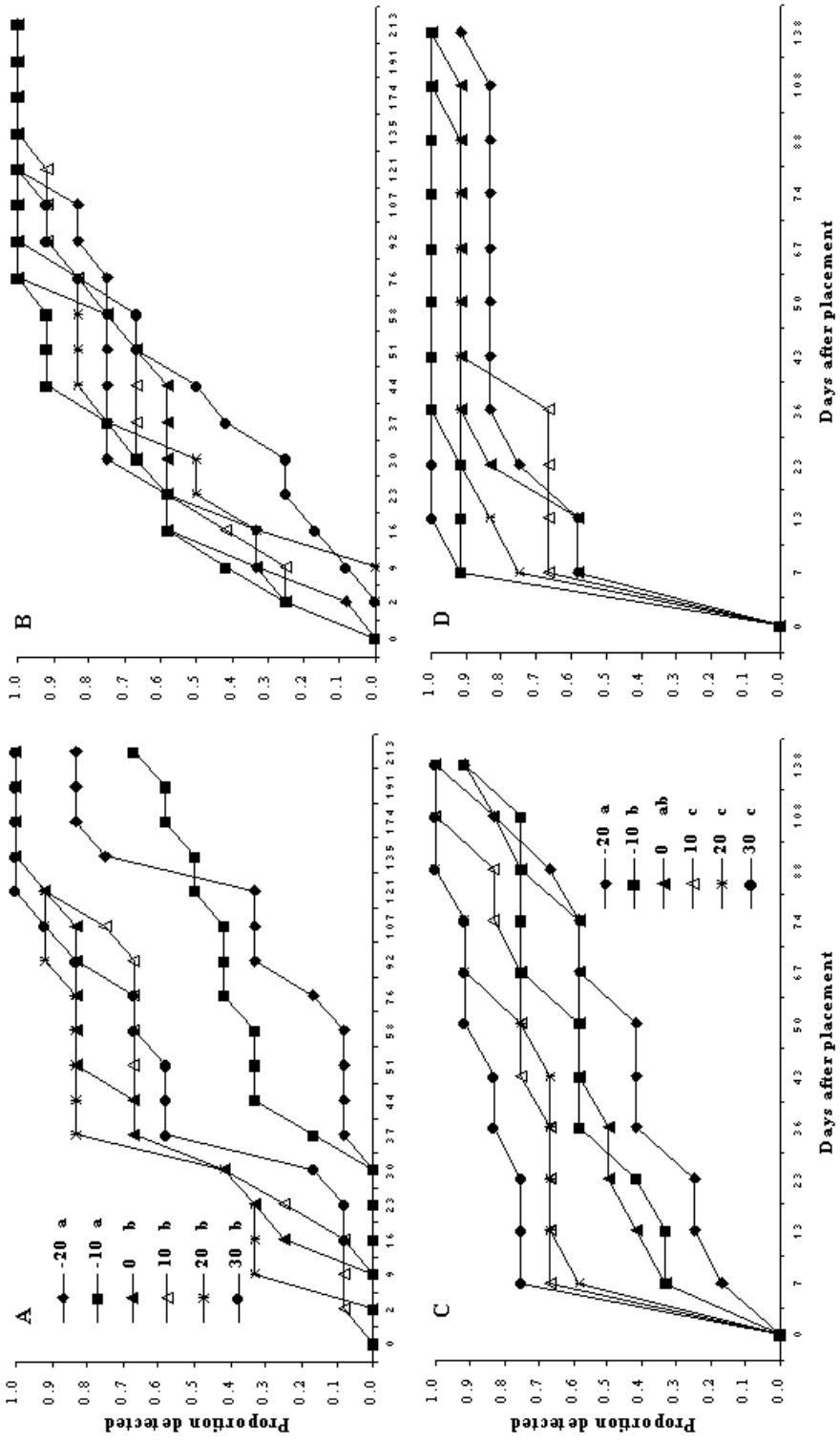

Fig. 3. 5 Proportion of piles of *Q. laurina* acorns detected through the time for each edge type and distance from the edge. Graphs A and B show the temporal trends of mean probability of detection for hard and soft edges in year 1. Graphs C and D show the temporal trends of mean probability of detection for hard and soft edges in year 2. Error bars have been omitted to improve the clarity of the figure. Different letters after the graphs legends indicate significant differences in the overall shape of the curves as determined by the log-rank comparisons ($P<0.05$).

Acorn removal, microhabitat and small mammal abundance

A positive correlation between acorn removal and total vegetation cover was found, pooling the data for both years (Fig. 3.6). However, this relationship was significant only for sites with hard edges (Wald χ^2=20.45; df=1; P <0.001). Neither height of the herbaceous strata, proportion of dead wood nor shrub cover (0.5 to 1 m) showed significant correlations with acorn removal (Logistic, P>0.05).

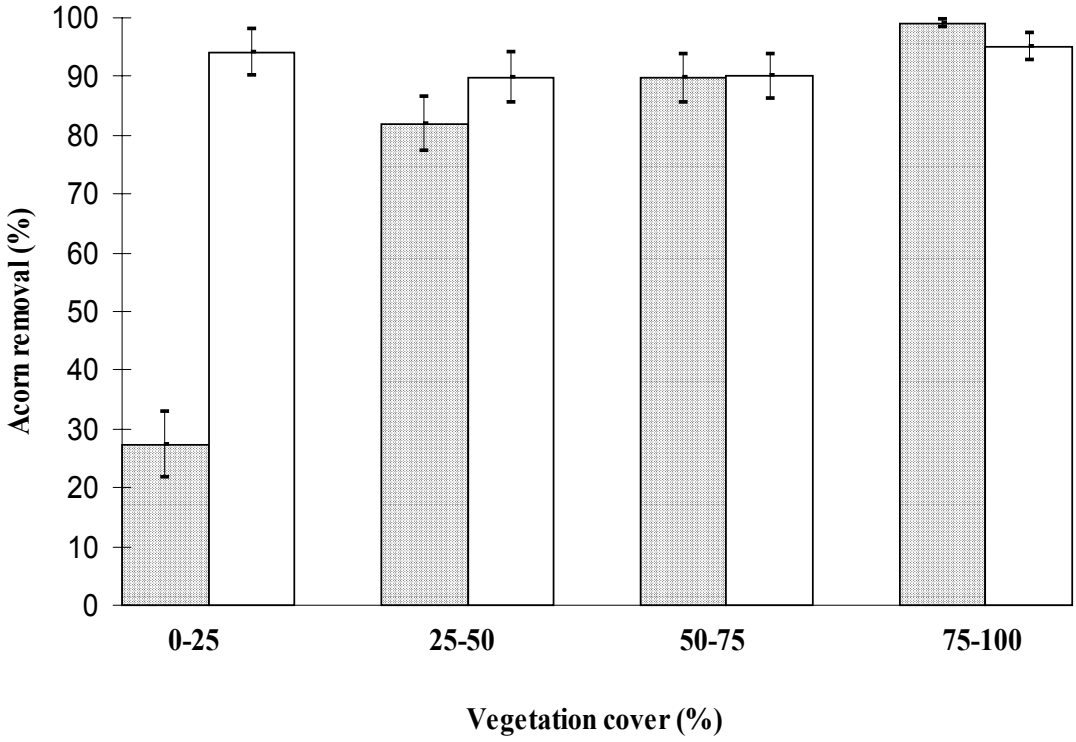

Fig. 3.6 Mean percentage of acorn removal (± 1 SE) of *Q. laurina* in relation to total vegetation cover at the point of the acorn pile, as a function of edge types: hard (shaded bars) and soft (open bars). Vegetation cover was transformed into a categorical value of four classes: 0-25% (n=36), 25-50% (n=41), 50-75% (n=37) and 75-100% (n=30). Means represent the mean acorn removal in both years.

Pooling data for the two years, a significant curvilinear relationship was found between percentage of acorn removal in each exclosure and average *Peromyscus* spp. trapping success (expressed as the number of captures per 100 trap nights) before and after the experiments (F=33.92; df=1,34; P<0.001; Fig. 3.7). Relationships between acorn removal and total trapping success of other species were not found (regression, P>0.05).

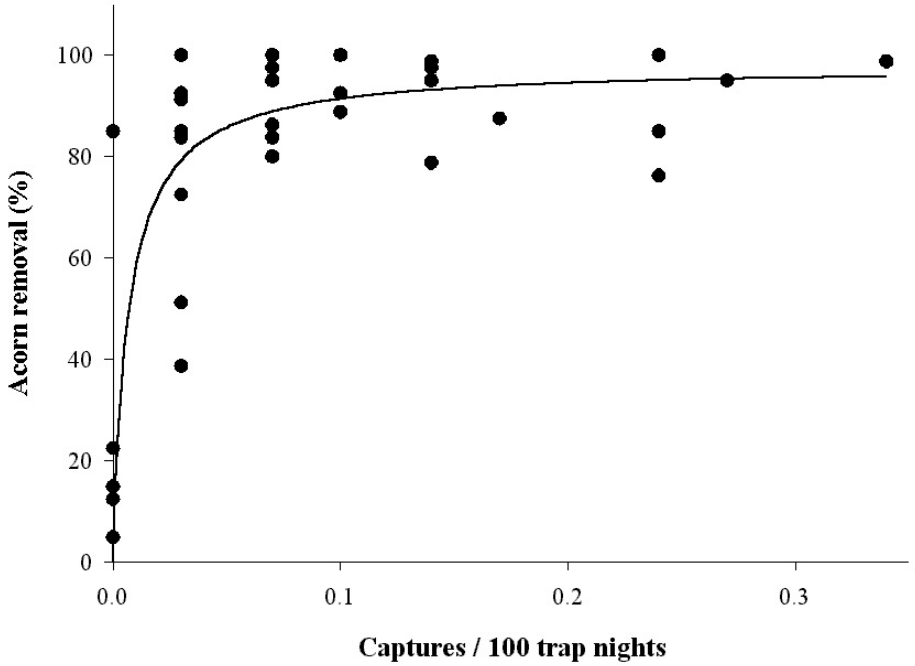

Fig. 3.7 Relationship (y=97.7*x/(0.007+x), R^2=0.50) between the mean percentage of acorn removal of *Q. laurina* and the mean trapping success (both variables were arcsine transformed) of *Peromyscus* species in the same distances from the edge before and after the experiments. Each data point represents the mean acorn removal observed in piles placed in both years in the six sites at different distances from the edge.

Fate of metal tagged acorns

Within 23 days after placement of 4060 metal-tagged acorns, 51.0% had been dispersed or eaten by small mammals. Only 2.2% (46) of the dispersed acorns and metal pieces were recovered with the metal detector, and these were distributed among 40 caches. From these acorns, the percentage of intact acorns recovered was 67.9% for the hard edge and 55.5% for the soft edge. Most of the acorns removed are likely to have been dispersed outside the explored area or to underground larder hoards by small mammals where I was unable to recover them with the metal detectors. As <3% of the acorns or metal tags were found, no statistical analysis was performed on these data.

Most acorns were cached singly. In the hard edge (PP), 24 caches were found. Of these, 21 had one acorn and three had two acorns. In the soft edge (PM), 16 caches were found, of which 14 had one acorn and two caches had two (Fig. 3.8). The mean dispersal distance of acorns in the two sites was similar (hard: 5.5 ± 0.9 m vs. soft: 5.3 ± 1.1 m), however the distribution of acorns and metal tags within the grasslands was different in the two sites (Fig. 3.8). In the soft edge, 12 acorns (8 intact and 4 eaten) were dispersed into the grassland at a maximum distance of 15 m. Rodents in the soft edge preferred to eat and disperse tagged acorns under dense herbaceous or shrub cover (64.4 ± 9.9%) crossing the edge, and most of the caches were located beneath the surface of the forest floor (2.6 ± 0.4 cm). In the hard edge, rodents preferred burying tagged acorns under the forest litter (5.2 ± 0.5 cm) along the edge and within the forest, and only four acorns (two intact and two eaten) were dispersed into the grassland at a maximum distance of 5.4 m.

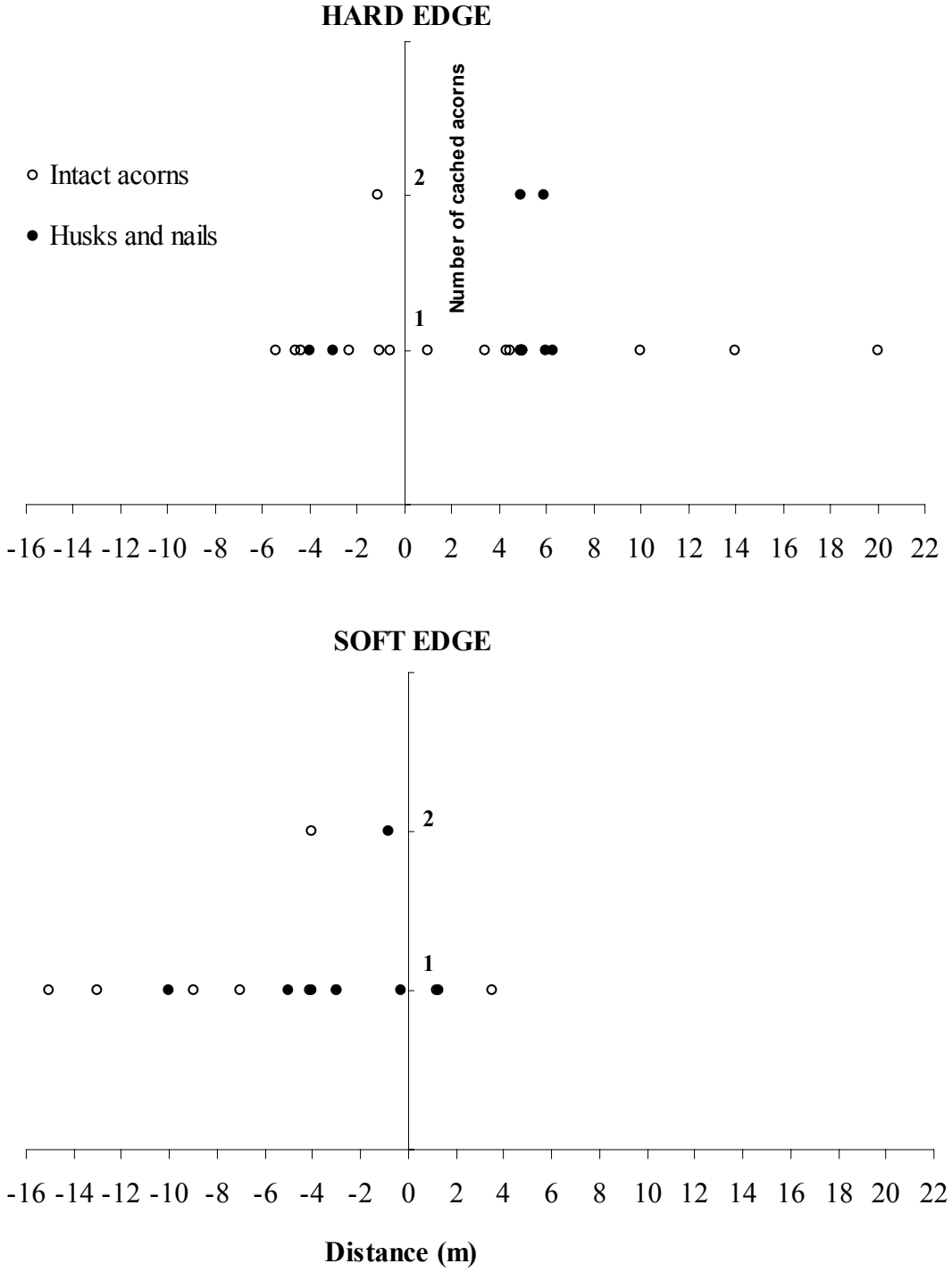

Fig. 3.8 Distribution of metal nails and tagged acorns of *Q. laurina* and *Q. candicans* along a forest interior-edge-grassland gradient at two sites, PM (soft edge) and PP (hard edge). The forest edge (0 m) was the initial tagged acorn supply. Negative distances indicate metres from the edge into the grasslands.

DISCUSSION

Edge effects on acorn removal: soft edges

The data presented in this study provide evidence that corroborates the hypothesis of edge permeability in sites with soft edges. Differences in acorn removal between edge types were exclusively due to the acorn removal patterns recorded in the grasslands. The decrease in acorn removal in the grasslands coincided with a decrease in *Peromyscus* spp. capture rate, suggesting that these species were the main acorn predators and/or dispersers as has been reported in previous studies mainly in North American oak forests (Elkinton *et al.* 1996; Bonfil & Soberon 1999; Plucinski & Hunter 2002; Kalcounis-Ruppell & Millar 2002; Schnurr *et al.* 2002). *Peromyscus* species in this study were evenly distributed along the forest-edge-grassland gradient in soft edges, suggesting there was no clear edge recognition by these animals in these sites. Higher seed predation in soft edges may reflect a tendency of acorn predators to avoid open areas, this being a behavioural adaptation to predators (particularly avian predators). Similarly, Fenske-Crawford & Niemi (1997) found higher nest predation by small mammals (including *Peromyscus* spp.) along soft edges than in hard edges in a forest dominated landscape.

It has been documented that individuals of some small mammal species decrease their activity in open areas (Anderson & Boutin 2002) and during full moon periods (Bowers & Dooley 1993). Individuals are more active under vegetation cover (Manson *et al.* 1999), or prefer to nest under vegetation with structural complexity (Kalcounis-Ruppell & Millar 2002) that can be used as shelter against predator attacks. Potential small mammal predators in the study area include grey foxes (*Urocyon cinereoargenteous*), opossums (*Didelphis virginiana*), Beared screech-owl (*Otus barbarus*), Great horned owl (*Bubo virginianus*), Mountain pigmy-owl (*Glaucidium gnoma*), Mottled owl (*Strix virginata*), Whiskered Screech-Owl (*Otus trichopsis* ssp. t*richopsis*), kestrels (*Falco sparverius*) and Godman's Montane Pitviper (*Cerrophidion tzotzilorum*) (Reid 1997; Howell & Webb 1999).

Few experimental studies have linked edge structure with the fluxes of small mammals and explored their consequences for forest regeneration. Cadenasso & Pickett (2000) studied the influence of vegetation structure on tree seedling predation by voles that penetrated into the forest interior from adjacent old-fields. They experimentally thinned the vegetation along the edge-forest interior gradient, but because of inadequate replication, they found only site-differences in the predation responses. At one site they found that voles preferred the intact plot, which they explained as a consequence of the removal of lateral branches in the thinned treatment, which caused an increase in herbaceous cover resulting in the tree seedlings becoming less obvious to the voles. Kollmann & Buschor (2002) found that predation of *Prunus avium* and *Viburnum lantana* was significantly higher near the forest edge only in sites with intact shrub cover; in sites where the shrub cover was removed, no such effect was found.

In this study, the vegetation cover in the grasslands of sites with soft edges, produced by different vegetation structures (tall herbs, shrubs, logs, etc.), provides a highly heterogeneous light environment at the soil surface. Microsites without ground vegetation cover in sites with soft edges did not affect the foraging behaviour of acorn predators as was recorded in the sites with hard edges. A positive correlation between acorn removal (data from both years) and vegetation cover over each group of acorns, was recorded only in sites with hard edges. This is a key finding of the present study, as it indicates that the vegetation cover surrounding the exposed microsites had an effect on their use by acorn predators and that habitat-mediated predation risk may operate through the amount of available vegetation cover at various spatial scales. Similar results obtained by Bowers & Dooley (1993) suggested that seed removal rates varied between open and covered microhabitats (<2 m), but these differences were only significant when considered in conjunction with larger scale features of the landscape (patch scale). At larger scales, both patch and landscape composition may affect the probability of small mammal presence by influencing habitat selection and dispersal (Song & Hannon 1999). The spatial range over which possible edge and cover effects can be detected should be explicitly considered in future studies (Kotliar & Wiens 1990; Donovan *et al.* 1997).

As a consequence of the preference of seed predators to use sites with vegetation cover, seed predation may often be higher in the presence of vegetation cover than in open sites such as grasslands, treefall gaps and bare ground (Mittelbach & Gross 1984; Webb & Willson 1985; Kikuzawa 1988; Myster & Pickett 1993; Hau 1997; Manson & Stiles 1998; Diaz *et al.* 1999; Schreiner *et al.* 2000; Kollmann & Buschor 2002). However opposing results have also been documented (Schupp 1988). Some studies have found that acorn removal is higher in forested than in open sites for *Q. mongolica*, (Kikuzawa 1988), *Q. crispilis*, (Quintana-Ascencio *et al.* 1992) and *Q. emory* (Hubbard & McPherson 1999) whereas other studies have shown acorn removal to be independent of overstorey vegetation for *Q. rubra* (Myster & Pickett 1993; Plucinski & Hunter 2002) and *Q. emory*; (Hubbard & McPherson 1999). In addition, acorn removal has also been reported to be much more intense when the acorns are placed on the soil surface than when buried in the soil or covered by a litter layer (Bossema 1979; Kikuzawa 1988; Crawley & Long 1995; Herrera 1995; Kollmann & Schill 1996; López-Barrera & González-Espinosa 2001) but see Gomez *et al.* (2003).

Edge effects on acorn removal: hard edges

In this study, in the sites with hard edges acorn removal did not present a negative edge effect, as was hypothesised. On the contrary, during the mast-seeding year, a trend toward higher acorn removal along the hard edges was recorded. Acorn predators did not avoid the edge; furthermore, trapping success of *Peromyscus* species was higher along the edge. This can be attributed to the herbaceous and shrub cover growing in the edge due to the increased incidence of lateral light in these open edges (see Chapter 2). In addition, individuals living in the forest patches may occasionally penetrate few metres into the neighbouring grasslands and their activity in these less-preferred habitats may be concentrated near the edge (Andren & Angelstam 1988). This is supported by the results using metal-tagged acorns in the hard edge; rodents moved acorns into the grassland only a few metres. Higher abundance of seed predators (such as *Peromyscus* species) at the edge may be attributable, among other causes, to: a) edges acting as travel corridors for animals,

b) higher abundance of fresh-fruiting plants may focus their search efforts along the edge (Restrepo *et al.* 1999), c) interspecific competition (Manson *et al.* 1998; Manson *et al.* 1999) and d) intraspecific competition (Pusenius *et al.* 2000; Anderson & Boutin 2002).

Failures to cross into a neighbouring habitat may be influenced by the organism's perception of the distance that must be travelled to reach another favourable patch (Lidicker 1999). To minimise predation, small mammals at the edge between two habitats should opt for the habitat having fewer open spaces and a relatively compact structure (Rodriguez *et al.* 2001). A matrix effect was found in this study as hard edges were impermeable to acorn predators during the mast-seeding year. Two individuals of *Peromyscus levipes* (10 and 20 m from the edge into the grassland) in hard edges were recorded in one trap session where there no was natural availability of acorns following the non-masting year (July 2002). This suggests that scarcity of resources within the forest may have had an effect on the foraging behaviour of this species and more individuals took the risk to travel to open sites without any cover and with greater exposure to predators.

Inconsistent edge effects have been reported for *Peromyscus* species owing to variation in a number of factors including edge vegetation, adjacent land use, region, ecosystem, predator assemblage, forest size and type. For instance, for *Peromyscus leucopus* different edge related responses have been reported in different studies: a positive edge effect (Manson *et al.* 1999), a negative edge effect (Wolf & Batzli 2002), and a matrix effect (Heske 1995). Horvarth *et al.* (2001) documented a positive edge effect on the abundance of *P. mexicanus* in a Neotropical forest in Chiapas, Mexico. In the current study, such an edge effect was not detected for this species. Interactions between small mammals species and distance from the edge have also been documented. Ostfeld *et al.* (1997) found that voles (*Microtus* spp.) had a strong, negative effect on seedling survival, but a positive indirect effect on seed survival by inhibiting seed predation by mice (*Peromyscus* spp.). They found that mice and voles had their strongest effects in different positions with respect to the forest-field edge.

Predictions of the long-term effects of edges on species of small mammals living in fragmented landscapes can be based on the habitat use of the species. For example species utilising the matrix between forest fragments and agricultural clearings (e.g. *Reithrodontomys* spp.) are advantaged by the fragmentation process, whereas forest specialists or species that require structural complexity (such as some *Peromyscus* spp.) tend to be vulnerable in fragments (Wolf & Batzli 2002). Here, trapping success was higher in forest edges (0.086) compared with the forest (0.074) and the grasslands (0.067). The trapping success reported in this study is approximately of the same magnitude as other studies in Neotropical forests (see review in Haines *et al*. 2000): 0.007 in pre-montane tropical forest, Costa Rica and 0.03 in the adjacent pastures (Haines *et al.* 2000), 0.085-0.257 in Shrublands in Hong Kong (Hau 1997), 0.045 in tropical montane forest in Chiapas (Quintana-Ascencio *et al.* 1992), 0.042 in forest edges and 0.018 in crops (Horvath *et al.* 2001).

Acorn production and survival

In spite of extensive studies of acorn crops in oaks, the data are insufficient to explain the principal causes of year-to year variation in acorn production (Sork *et al.* 1993; Koenig *et al.* 1994; Crawley & Long 1995). The rate of acorn survival varied markedly between years; during the mast seeding year, 30% of acorn survival was recorded 174 days after release, whereas during the non-mast seeding year, the same level was reached after 92 days of exposure to predators. These periods of time differ markedly from other studies that have reported more rapid acorn removal: 24 hrs after exposure (Shaw 1968), 2 days (Plucinski & Hunter 2002), 7 days (Herrera 1995), 10 days (Li & Zhang 2003) and 35 days (Bonfil & Soberon 1999).

In this study, the higher probabilities of acorn survival during the masting year (year 1) can be attributed to a combination of increased food production (predator satiation) and the low abundance of small mammals (trapping success of 0.004) compared with year 2 (trapping success of 0.098)**.** Higher seed escape from predators (small mammals and insects) during the mast-seeding period, and therefore higher seedling recruitment, have been documented in several studies in temperate

forests for Q. *robur* (Jensen 1982), *Quercus liaotungensis* (Yu *et al.* 2003) and *Q. rubra* and *Q. alba* (Wolff 1996); however a long-term study of *Q. robur* show that there is low predictability in this trend (Crawley & Long 1995).

Wolff (1996) and McShea (2000), using a 14-year and 12-year dataset respectively, found that during the mast seeding years, small mammals (*Peromyscus* spp., *Tamias striatus* and *Sciurus carolinensis*) stored acorns that lasted throughout winter. This resulted in winter breeding and increased winter survivorship of mice; consequently high densities of animals were observed the following spring and summer. In subsequent years, low acorn production resulted in population declines and several years of low rodent densities. Complex interactions resulting from these population fluctuations of small mammals have been documented between acorn crops and bird nest predation (McShea 2000), the transmission of Lyme disease (Ostfeld *et al.* 1996; Elkinton *et al.* 1996) and decreased tree seed survival of non-oak species during non mast seeding years (Schnurr *et al.* 2002)

Spatiotemporal variation in predator satiation has also been documented. Boucher (1981) reported a lack of correlation between individual tree crop size and the survivorship of acorns in oak forest; only dense oak stands provided sufficient acorns to satiate the mammals. He also suggested that the lack of a satiation effect at the individual level is because satiation is operating at the population level. Curran & Webb (2000) and Curran & Leighton (2000) documented that satiation of nomadic and resident predators occurs at the landscape level. They found that mast fruiting of several *Dipterocarpaceae* species (48 species) exhibits highly synchronous mast seeding as a consequence of directional selection by seed predators. Forest fragmentation can have effects on the final outcome of mast seeding years, as without sufficient quantity and spatial extent of seed production, increased populations of seed predators may destroy all seed produced in a local stand (Curran *et al.* 1999). For example Santos & Telleria (1997) found that acorn consumption (*Q. ilex*) by mice was much higher in small stands than in larger stands. In the area of the current study, mast-seeding was observed in more than one municipality and for more than one oak species. Further evaluation of reproductive synchrony of tree

species in areas with different degrees of fragmentation would enable the probabilities of tree recruitment at the landscape scale to be evaluated, together with implications for the coexistence of so many oak species in the region.

Oak dispersal

Although small mammals removed more than half of the tagged acorns, so few seeds were relocated that is difficult to draw any strong inferences about the ultimate fate of acorns. However, the results support the concept of permeability of soft edges. Small mammals dispersed acorns into the grassland in the site that has a soft edge, whereas in the hard edge, the dispersal of seeds was mostly concentrated along the edge and within the forest. Few studies have studied oak dispersal into grasslands. Hubbard & McPherson (1999) found that approximately 7% of *Q. emory* acorns were dispersed 50 m in the adjoining grassland and Kollmann & Schill (1996) reported low experimental acorn dispersal of *Quercus petraea* (0.4%) into an abandoned grassland.

Calculating the number of intact acorns relative to the total number of metal pieces recovered with or without acorns, the overall acorn survival in this study was 63% (29/46). This is a very high value compared with other studies using similar methods. Jensen & Nielsen (1986) reported 2.5% (12/485) survival at a maximum distance of 34 m and Li & Zhang (2003) reported 23% (68/228) and 10% (10/101) acorn survival during two consecutive years, respectively, at a maximum dispersal distance of 23 m. However, these results should be compared with caution as the final fates of acorns varied markedly with the time period of the study. For example, Miyaki & Kikuzawa (1988) found that after 17 days of the first check, mice relocated 29% of the acorns, and 7 months after the first check, only one acorn remained and germinated among the 64 acorns that were hoarded. In this study, sites were searched soon after removal and no replication through time was performed. Also, studies differed in the availability of food at the moment when tagged acorns were released in the field. For example, Sork (1984) exposed tagged acorns to predators during

summer, when there is low availability of seeds, so it is not surprising that she reported low acorn survival (0.9% at a maximum dispersal distance of 19 m).

Acorn caches can be buried under soil or litter, or placed in burrows, tree holes or nests and can consist of a few large caches (larderhoards) or many small-scattered caches (scatterhoards), as occurred in this study. Rodents rely on olfaction to relocate seeds (Price & Jenkins 1986), therefore the probability of relocating caches of single acorns is low, increasing the probability of escaping predation. This is supported by findings relating to the density dependence of acorn survival. Boucher (1981) found higher survival of single isolated acorns of *Q. oleoides* in a tropical lowland forest than piles of 10 or more acorns; the same pattern was reported for *Q. rugosa* acorns (Bonfil & Soberon 1999). Scatterhoarding (caches from one to seven acorns) has been documented in some studies for *Q. liaotungensis* (Li & Zhang 2003) and *Q. mongolica* (Miyaki & Kikuzawa 1988). However, Jensen & Nielsen (1986) reported that the density of caches (1 to 16 acorns) of radioactive tagged acorns decreased with increasing distance from the seed source.

Data presented in this study suggest that rodents preferred to cache acorns under the dense shrub cover in the grassland of the sites with the soft edge. Li & Zhang (2002) found that rodents preferentially buried tagged acorns under dense shrubs and at the edge of shrub cover, but never in bare ground. Acorn transportation into the grasslands by rodents is therefore determined by current vegetation cover. The interplay between seed predation and seed dispersal, as influenced by vegetation cover, will therefore determine the success of oak dispersal (Price & Jenkins 1986). The balance between these processes has seldom been investigated in open areas, although studies have documented that seedlings of oaks are abundant in abandoned old-fields or shrub fallows (González-Espinosa *et al.* 1991; González-Espinosa *et al.* 1997), primarily as a result of rodent activity (Jensen & Nielsen 1986; Kollmann & Schill 1996).

In this research, during the mast-seeding year the proportion of acorns that were not removed by small mammals and germinated or produced seedlings after 213 days

was similar (31.5 vs. 30.9%) among the grasslands (-10 and -20 m) and within the forest interior (0, 10, 20 and 30 m). However, in forest stands rodent predation has been reported as a major cause of low regeneration of oaks. In such situations acorns that escape vertebrate predation suffer insect and fungal attack or desiccation (Leiva & Fernandez-Ales 2003). Herrera (1995) found of 221 acorns buried only two seedlings survived the first year, and none survived the second year. Jensen & Nielsen (1986) reported that 2.4% (12) of the radioactive tagged acorns of *Q. robur* and *Q. petraea* developed into seedlings and Barik *et al.* (1996) reported than 98% of the acorns were consumed or transported by rodents and insects while fewer than 1% germinated.

Rodents have only recently begun to be investigated as seed predators and/or dispersers in the Neotropics, despite their importance in Neotropical montane forests (Boucher 1981; Brewer & Rejmánek 1999). While dozens of *Quercus* species occur in tropical Mexico and Central America, most studies of oak regeneration and dispersal have been undertaken in temperate forests, where relatively few oak species occur. This is the first research that has studied the interaction of acorn predators and/or dispersers and acorn survival, together with a consideration of the temporal and spatial variability of this interaction. Data presented here indicate that whether *Peromyscus* spp. are net predators or dispersal agents depends on the temporal variability of the acorn crops and the occurrence of mast seeding years.

This study contributed to the development of a theory of edge structure and edge function (Laurence *et al.* 2001). The results of these experiments indicate that the structure of the forest edge and the adjacent habitat, in combination with the nature of the flux (small mammal species), determined edge permeability. Hard edges may act as a barrier to the flux of acorn predators and/or dispersers, limiting the dispersal of acorns in these sites, while soft edges act as a permeable membrane to small mammals, increasing the probability of oak invasion into the abandoned grasslands.

The conclusion is that mosaic landscapes consisting of small agricultural clearings, produced by a land use cycle of abandonment and use of clearings, result in spatial

variation in the mobility of acorn predators and/or dispersers. Oak dispersal into clearings will be determined by the combination of factors including the occurrence of mast-seeding years, the vegetation cover of the clearing, and fluctuations in small mammal density. As oak regeneration is higher in abandoned grasslands or shrub fallows than within the closed oak canopy (Chapter 6), the maintenance of traditional land use systems (small-scale disturbance and shrub fallow) in these montane forest landscapes is important to allow oak tree recruitment and forest regeneration, and the conservation of small mammal populations, especially those species that are forest specialists or use small-scale heterogeneous landscapes.

CHAPTER 4: Edge effects in a forest mosaic: experimental tests of post-dispersal acorn removal.

ABSTRACT

Forest edges created by scattered-patch clear cutting have become common in tropical montane cloud forests in the Highlands of Chiapas (2300-2450 m), Mexico. I hypothesised that forest edges may influence regeneration of oak species, which are canopy dominants in these forests, by affecting the activities of small mammal species. To test this, acorns of different species that varied in germination timing were offered to predators and/or dispersers at different positions along replicated forest edges during two consecutive years. I investigated the effects of 1) edge type (hard and soft), 2) distance from the edge (0, 15, 30, 45 and 60 m inside forest fragments) and 3) oak species on the rate of acorn removal by small mammals. During the non-masting year, acorn removal was affected by the interaction of edge type and distance from the edge, with acorn removal being highest near hard edges compared to the forest interior. As predicted, acorn removal was greater along soft than along hard edges. Patterns of acorn removal and damage varied between years and between oak species. This study supports previous studies of squirrel preferences for acorns that have early germination rather than acorns that exhibit dormancy, however these patterns may change with variation in acorn abundance. These results suggest that patch clear cutting affects regeneration processes within forest fragments, by influencing the activities of small mammals, but the nature of this effect also depends on acorn abundance and the characteristic of the forest edge created.

INTRODUCTION

In the Highlands of Chiapas, as in other neotropical montane forests, agriculture plays a major role in the dynamics of landscape fragmentation (Nigh 1975; Collier 1975; De Jong *et al.* 1999; Ochoa-Gaona & González-Espinosa 2000). Within the fragments of tropical cloud montane forest, indigenous farmers practising shifting

cultivation for centuries have created a forest mosaic of patches (0.5-2 ha) of secondary vegetation in different successional stages surrounded by forest (González-Espinosa *et al.* 1991). Within this dynamic landscape, forest edges have become common habitats (Ochoa-Gaona & González-Espinosa 2000). There is increasing recognition that forest edges should be more intensively studied in fragmented landscapes (Wiens *et al.* 1993). However, most previous fragmentation studies have focussed on edge effects within the forest community at larger spatial scales and have been conducted in preserved forest fragments immersed in a matrix of disturbed habitats (Laurance 1997; Laurance & Bierregaard 1997; Benitez-Malvido 1998; Laurance *et al.* 1998). There is a lack of understanding about edge effects in dynamic forest mosaics at smaller spatial scales.

Recently, studies have suggested the importance of the type of vegetation adjacent to forest fragments as a modulator of edge effects (Didham & Lawton 1999; Gascon *et al.* 2000). Mesquita *et al.* (1999) found that edge effects on tree mortality penetrated further into pasture-bordered edges (60-100 m) than those bordered by shrub or tree fallows (40-60 m). Adjacent vegetation can create edges with different structural and ecological characteristics. Hard edges may result from abrupt transitions between the open area and the forest, whereas soft edges may arise from the gradual transition between abandoned crops or shrub fallows.

Small mammal communities respond in different ways to various types of vegetation (Andren 1994; Bayne & Hobson 1998; Menzel *et al.* 1999; Harrington *et al.* 2001), therefore forest edges adjacent to different vegetation types can evoke different responses (Piper *et al.* 2002). This has been documented in studies relating to nest predation by small mammals. Negative forest edge effects on nest predation tend to be consistent in agricultural or urban landscapes (with more hard or abrupt edges), whereas studies in forested landscapes or forest mosaics (with more soft edges) have often documented little or no edge effects (Donovan *et al.* 1997; Song & Hannon 1999; Piper *et al.* 2002). Fenske-Crawford & Niemi (1997) found that nest predation by mammals near soft edges and away from the edge was significantly higher than near hard edges, however other studies have not found such a link between edge type

and predation rate (Fleming & Giuliano 1998; Song & Hannon 1999). Understanding how mammal movement is influenced by the spatial configuration of landscape habitats is critical but very little is known about how small mammals respond to edges with different structures (Lidicker & Peterson 1999; Manson *et al.* 1999).

Regeneration of oaks relies on animals such as squirrels as dispersers of acorns. Squirrels are traditionally associated with forest habitats and their activity is related to vegetation cover across forest mosaics (Rodriguez & Andren 1999; Fisher & Merriam 2000). This interaction provides an opportunity to evaluate the effects of different edge types on the foraging behaviour of acorn predators and/or dispersers and its consequences for acorn survival. Despite the high biological, cultural and economical importance of oaks and small mammals in Neotropical montane forests (González-Espinosa *et al.* 1995; González-Espinosa *et al.* 1995; Horvath *et al.* 2001), to my knowledge no previous research has evaluated their interaction in these systems and how it is affected by forest fragmentation.

Squirrels and mice may significantly affect oak recruitment (Boucher 1981; Jensen & Nielsen 1986; Kikuzawa 1988; Callaway 1992; Herrera 1995; Santos & Telleria 1997; Smallwood *et al.* 1998; Steele & Smallwood 2002). Some squirrel species tend to store acorns in larder-hoards or in cache sites that are unsuitable for germination and recruitment, but other Sciurid species scatter-hoard acorns in individual cache sites which are just below the ground surface and are likely to contribute to oak dispersal (Steele & Smallwood 2002). The foraging behaviour of squirrels has been studied as a function of: a) acorn perishability (Hadj-Chikh *et al.* 1996), b) acorn tannin concentration (Steele *et al.* 1993), c) acorn fat concentration (Steele *et al.* 1999), d) acorn size and shape (Hadj-Chikh *et al.* 1996), e) acorn species (Steele *et al.* 2002) and f) the presence of weevil infected acorns (Steele *et al.* 1996). However, there is no experimental evidence describing how the interaction between squirrels and acorns can be affected by distance or type of forest edge present which could in turn affect the dispersal and spatial distribution of oaks.

In this study, acorn removal rates were compared at different distances from hard and soft forest edges (details of the vegetation structure are given in Chapters 2 and 3) over two consecutive years. A general hypothesis is that as structural similarity increases between two adjacent stands, the edge created between the stands becomes less abrupt and the edge may be more like a forest interior. Based in this assumption, I hypothesised that along hard edges, distance from the forest edge into the forest patch will determine rates of acorn removal because small mammals will avoid approaching the edge, while in fragments with soft edges, acorn removal will be homogeneous regardless of distance from the edge since rodents will use all available forest edge and forest habitat.

Acorn characteristics are now known to have a major influence on the dispersal of oaks. Oaks can be grouped into two subgenera on the basis of acorn characteristics. Acorns of white oaks (subgenus *Leucobalanus*) mature in the first season and germinate immediately after they have dispersed, whereas acorns of red oaks (subgenus *Erithrobalanus*) usually mature in the second season and germinate in the spring after a period of cold treatment. Studies have suggested that squirrels preferentially cache acorns of the red oak group, but immediately consume acorns of the white oak group (Fox 1982; Steele *et al.* 2001). Recently it has been suggested that differences in germination schedules (including within-subgenus differences) directly affect squirrel caching preferences (Smallwood *et al.* 2002). These findings relating to differences in germination schedules and their consequences for acorn survival suggest that acorn removal will occur at a higher rate and a greater extent in acorns with autumn germination compared with acorns that exhibit dormancy. This prediction was tested in the current investigation.

METHODS

Experimental plots

For purposes of this study six sites with grasslands and adjacent pine-oak forest (three sites with hard edges and three sites with soft edges) were chosen. For detailed information about the study area and experimental plots see Chapters 2 and 3.

Potential acorn predators and/or dispersers

Grey squirrels (*Sciurus aureogaster* Cuvier, 1829) and red squirrels (*Sciurus deppei* Peters, 1863) were observed on the study sites during the experiments (Reid 1997). Squirrels in this area are intensively hunted for human consumption, therefore squirrels avoid humans and few observations were recorded. Other potential acorn consumers found in the study area were *Peromyscus levipes*, *P. aztecus, P. mexicanus* and *P. zarhyncus* (detailed data concerning small mammal abundance and distribution are provided in Chapter 3). When possible, evidence of acorn consumption indicated by incisor marks on acorn cotyledons was recorded to determine the predominant predator type.

Acorns

From September 2000 to March 2002 the natural pattern of acorn production was followed. The first year acorn fall took place in early September 2000, which was a masting year (161.1 ± 19.4 acorns m^{-2}), whereas the second year was a delayed fall and acorns fell until November 2001. Acorn production the second year was relatively low (21.3 ± 2.9 acorns m^{-2}; see details in Chapter 3). During these periods acorns were collected and viability was tested by floating them in water, which is a reliable method to identify damaged acorns typically avoided by rodents (Gribko & Jones 1995); only those which sank were subsequently used in seed predation trials. Acorns of approximately equal size were chosen for each removal trial. The main characteristics of the acorns used in this study are summarised in Table 4.1. *Q.*

crassifolia, although a red oak, has unusual acorns that germinate in autumn; acorns of this species were included in the experiment.

Table 4.1 Main characteristics (means ± 1 SE) of the *Quercus* species used in the experiments. Germination trials were performed in the laboratory (see details in Chapter 5). Germination values (see Chapter 5 for details) were obtained after 220 days for *Q. laurina* acorns, 102 for *Q. candicans,* 58 for *Q. crassifolia* and 30 for *Q. segoviensis*. Acorn measurements were made from 100 recently collected seeds of each species before the flotation test.

	Species	Group	Acorn dormancy	Acorn germination (%)	Acorn diameter (cm)	Acorn Mass (g)
Year 1	*Q. segoviensis*	White	No	89.4±1.4	2.08±0.03	5.37±0.15
	Q. laurina	Red	Yes	99.2±0.5	1.35±0.02	1.80±0.06
Year 2	*Q. crassifolia*	Red	No	98.7±1.3	1.26±0.02	1.61±0.05
	Q. candicans	Red	Yes	76.0±8.3	1.78±0.02	3.55±0.09

Acorn removal trials

The effects of acorn species, distance from the forest edge, and edge type (hard vs. soft edge) on acorn removal rates were examined. In each experimental plot, five 50 m-long line transects were established 15 m apart, parallel to the forest edge (0, 15, 30, 45 and 60 m from the edge into the forest). Three trees (≥30 cm dbh) were selected randomly along each line transect with no less than 10 metres between them. Species and dbh were recorded for each tree (Appendix 3). Metal dishes (20 x 25 cm) with acorns raised above the ground were used to create feeding trays available to squirrels and other arboreal rodents. A dish was nailed to each tree at 1.6 m above the ground. The dishes were not protected against acorn removal by birds, but observations of the jays foraging behaviour suggest that birds tend to remove acorns from the canopy or from isolated trees in open grasslands. Although the use of these artificial dishes may not reflect natural conditions, they were used consistently across all treatments, and thus can be used to document the different factors affecting

removal rates and the relative contribution of arboreal rodents in acorn predation or dispersal.

Between October 2000 and January 2001 (year 1), 10 acorns of each species (*Q. segoviensis* and *Q. laurina*) were placed on each dish. The survival of seeds was monitored each week. At the end of the experiment (when most of the acorns of at least one species had been removed or damaged) I analysed the damage type of the remaining husks and gnawed acorns on the dish. Remaining acorns were scored as a) intact, b) germinating, c) gnawed, d) gnawed and germinating, e) insect and fungi damaged and f) desiccated. I considered missing acorns as removed and not predated, because their final fate was uncertain. To compare the temporal variance of the removal rates this experimental design was repeated during December 2001 to February 2002 (year 2). Due to differences in acorn availability I used acorns of *Q. candicans* and *Q. crassifolia.* These two species have contrasting germination times and acorn size (see Table 1).

Statistical analysis

Dependent variables (numbers of acorns removed) were discrete rather than continuous, therefore patterns of predation were analysed using categorical modelling. The CATMOD procedure, analogous to ANOVA but with categorical data represented in contingency tables, was used in these analyses (SAS v. 8.0). The log-linear model included the effect of edge type (hard and soft) and distance from the edge (0, 15, 30, 45 and 60 m). Their interaction was also tested. Sampling zeros in the contingency tables were replaced by 10^{-20} to ensure that the sampling zeros were not treated as structural zeros in the analysis and maximum likelihood estimation was used (as suggested by SAS 1989; Folke 2001). Statistical significance was determined by chi-squared tests of the information matrix from the maximum likelihood calculations. The effect of species could not be included within this analysis as the proportion of seeds remaining of each species was not independent since both species were placed in the same dish.

The proportion of acorns removed from the dishes was transformed into a categorical variable with three levels (low: 0-33%, medium: 33-66% and high removal: 66-100%). Second year data appeared to be bimodal (all or most of the seeds were either present or missing), therefore acorn removal was assigned to two levels (low: 0-50% and high removal: 50-100%).

For the masting year data (year 1) I tested two additional response variables: a) the proportion of acorns damaged *in situ* by squirrels and b) the proportion of dishes showing any evidence of foraging. These variables were not considered in the non-masting year (year 2) because most dishes were disturbed and the acorns were removed.

In a second analysis, the effect of oak species on seed survival and damage *in situ* was tested using Chi-Square tests (crosstabs procedure, SPSS v. 10.0.1). This test forms two-way tables and provides measures of association between categorical variables.

A final analysis explored temporal curves of probability of detecting acorn piles controlling for the experimental factors: edge type and distance from the edge using the Wilcoxon-Gehan test and pairwise comparisons (life tables procedure, SPSS v. 10.0.1). In the text, means are given ± 1 SE unless otherwise stated.

RESULTS

Edge type and distance from the edge

During the masting year (year 1), after 12 weeks of exposure to predators, acorn removal and acorn damage *in situ* were not significantly affected by the edge type or distance from the edge or by their interaction (CATMOD, $P>0.05$; Table 4.2, Fig. 4.1a). There was no evidence of edge type and distance from the edge influencing the chance of an acorn dish being detected (CATMOD, $P>0.05$; Table 4.2).

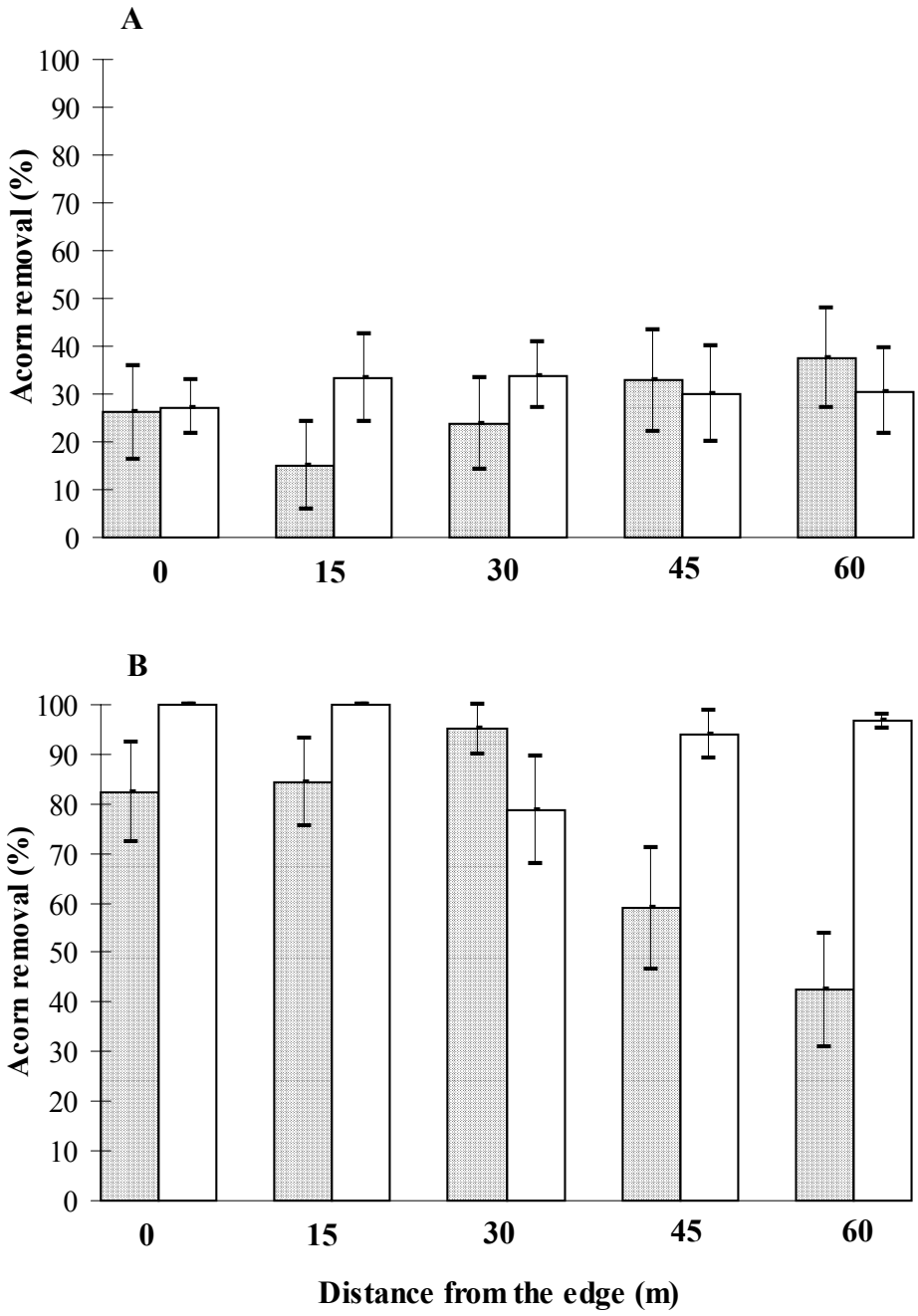

Fig. 4.1 Effect of edge type, hard edges (shaded bars) and soft edges (open bars), and distance from the edge on acorn removal patterns. A) Masting year (year1) and B) Non-masting year (year 2). Error bars represent ± 1 SE.

Table 4.2 Results of the categorical modelling analysis of the acorn removal at the end of the experiments in year 1 (2000-2001 a masting year) and year 2 (2001-2002 a non-masting year). The experimental factors were edge type (hard and soft) and distance from the edge (0, 15, 30, 45 and 60 m).

Experiment:		**Year 1**						**Year 2**	
		Acorn removal		**Acorn damage**		**Dish encounter**		**Acorn Removal**	
Source of variation	df	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Edge type	1	1.75	0.185	2.38	0.123	0.42	0.515	4.47	0.035
Distance	4	3.88	0.423	1.53	0.821	0.93	0.921	16.89	0.002
Edge type x distance	4	4.25	0.374	8.33	0.080	1.71	0.789	10.60	0.031

In the non-masting year (year 2), after 10 weeks of exposure to predators, there was a significant interaction between edge and distance from the edge affecting acorn removal (Table 4.2, Fig. 4.1b). In sites with soft edges all the acorns were removed near the edge while at 30 m from the edge there was a decrease in acorn removal. As expected acorn removal at the edge and near the edge was higher in sites with soft edges than in sites with hard edges (Fig. 4.1b). However, contrary to initial predictions in sites with hard edges, acorn removal was higher near the edge and at intermediate distances, than in the forest interior (45 and 60 m from the edge).

In year 1, none of the experimental factors had a significant effect on the probability of detecting acorn piles (CATMOD, $P>0.05$). During the non-masting year (year 2), temporal patterns of acorn piles detection were affected by the interaction of edge type and distance from the edge. In sites with hard edges, detection rates differed significantly between distances from the edge (Wilcoxon-Gehan $\chi^2 =14.84$; df =4; $P=0.005$). Tests comparing each pair of distances showed that dishes were discovered faster near the edge (0 and 15 m) than in the forest interior (30, 45 and 60 m; Fig. 4.2a). However, in sites with soft edges, the rate of detection of acorn piles was not affected by distance from the edge (Wilcoxon-Gehan $\chi^2 =6.78$; df =4; $P=0.148$; Fig. 4.2b).

Acorn species

Acorn fate at the end of the first experiment (year 1) is shown in Fig. 4.3. Gnawed remains of acorns clearly showed that squirrels were the main predators in year 1. A proportion of acorns from *Q. segoviensis* germinated during the experiment and some of them exhibited cotyledon damage. Whole and non-germinating acorns were more common for *Q. laurina. Q. segoviensis* acorns displayed a higher rate of germination but are also larger than *Q. laurina* acorns. In the second year I contrasted larger acorns with dormancy (*Q. candicans*) and smaller acorns with early germination (*Q. crassifolia*) with the aim of testing the effects of size and dormancy on acorn survival, however both species were removed rapidly during the second year so I was not able to make this comparison.

Acorn removal was higher for *Q. segoviensis* (34.0 ± 3.7%) than it was for *Q. laurina* (22.4 ± 3.1%; Chi-Square tests, χ^2=8.47; df=2; P = 0.014). The number of damaged acorns within the dishes showed the same trend (21.5 ± 2.7% vs. 4.4 ± 1.0%; χ^2=31.74; df=2; P<0.001; Fig. 4.3).

Masting vs. non-masting year

Total removal during the masting year (year 1) was lower than in the non-masting year (28.0 ± 2.4% vs. 84.7 ± 2.2%). However, the proportion of remaining acorns that was damaged by squirrels was higher in the masting year compared with the non-masting year (12.9 ± 1.6% vs. 1.3 ± 0.4%), implying that they partially ate more acorns *in situ* when food was widely available, but completely removed acorns when food was scarce.

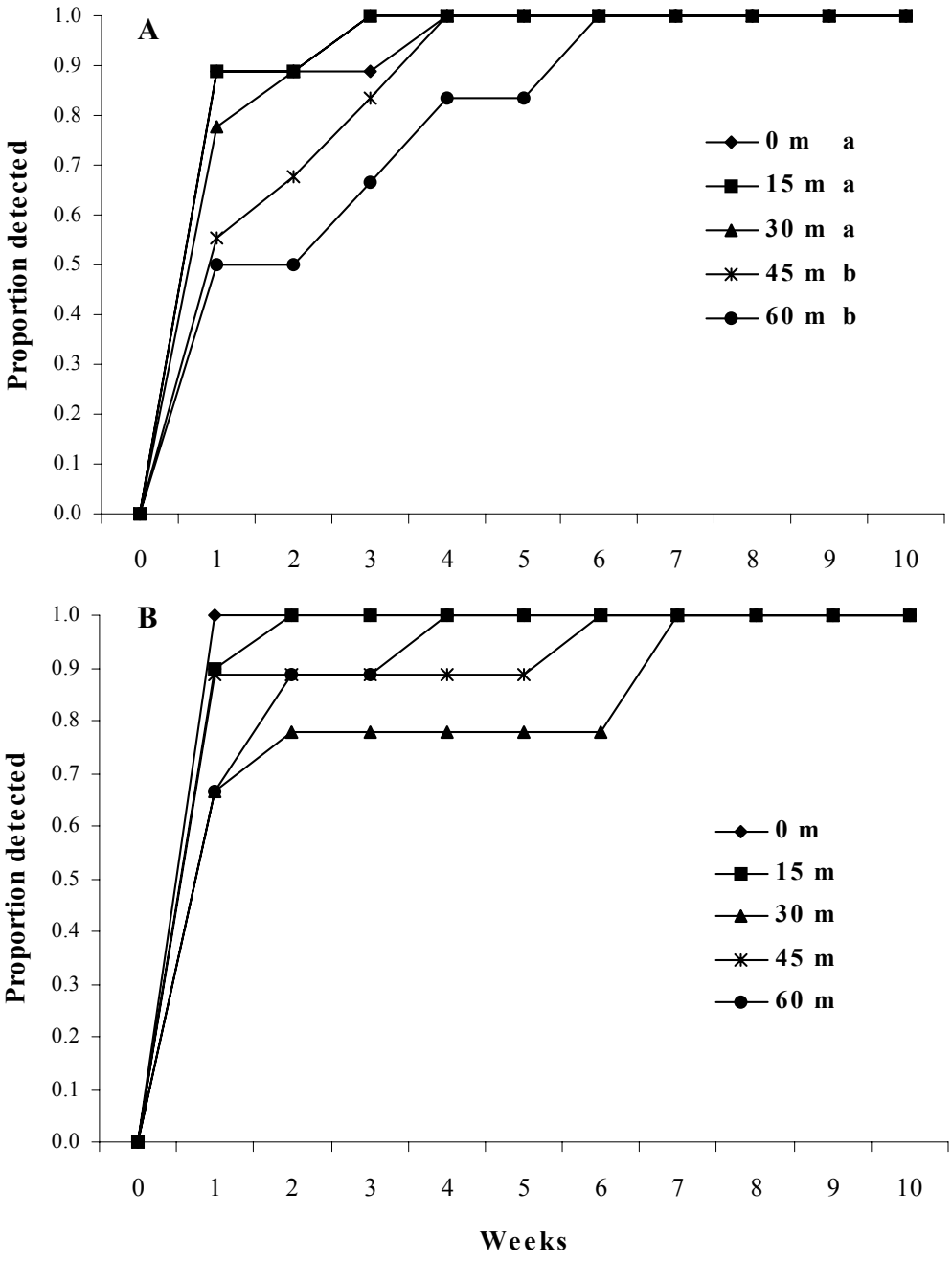

Fig. 4.2 Mean proportion (± 1 SE) of dishes of acorns detected through the time as a function of edge types, A) hard edges and B) soft edges, and distance from the edge. Different letters after the graph legend in the hard edges indicate significant differences in the overall shape of the curves as determined by Wilcoxon-Gehan pairwise comparisons (P<0.05).

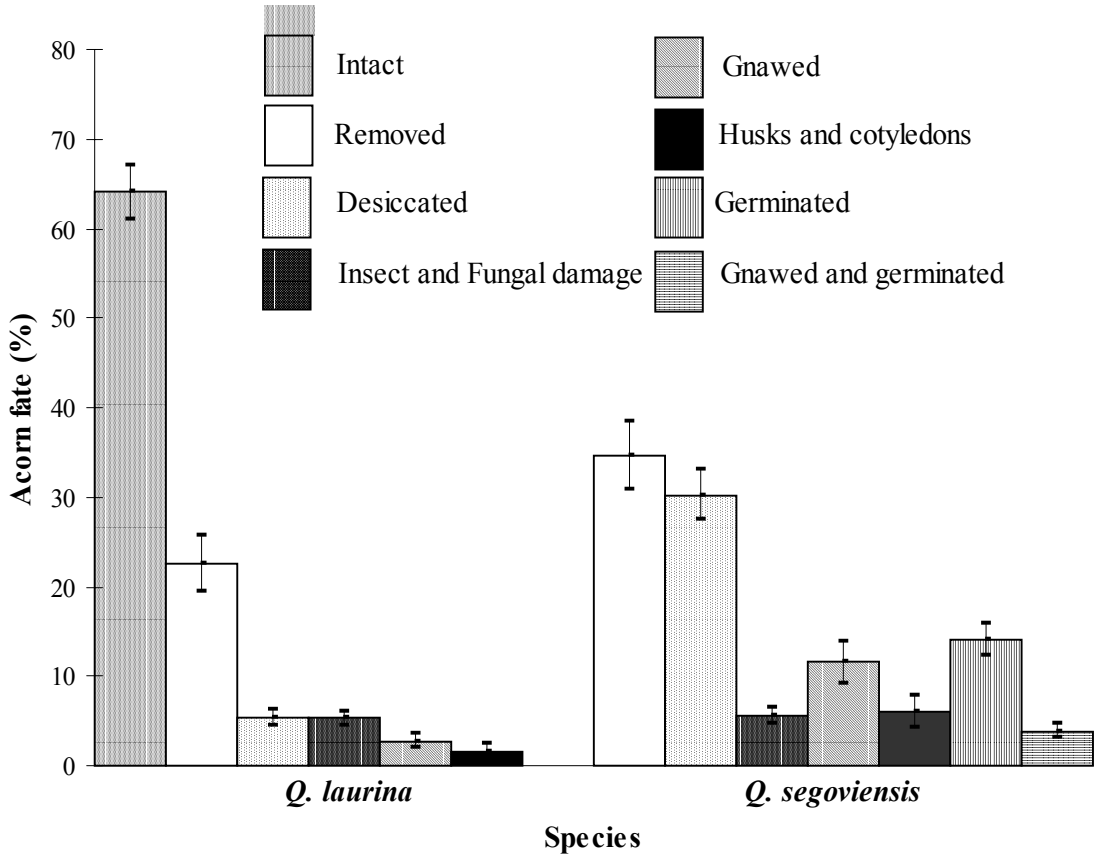

Fig. 4.3 Final fates of acorns for *Q. laurina* and *Q. segoviensis* after 12 weeks of exposure to predators during the masting year (year 1). Error bars represent ± 1 SE.

DISCUSSION

Edge type and distance from the edge

This study showed that adjacent vegetation type has an effect on the foraging behaviour of acorn consumers within the forest patches and therefore is affecting the probabilities of oak regeneration near the edge. However, the spatial patterns of acorn removal differed between mast and non-mast years. Previous studies of seed removal have found that the importance of microhabitat use by seed predators varies as a function of the availability of food (Willson & Whelan 1990; LoGiudice & Ostfeld 2002). Quintana-Ascencio *et al*. (1992) found in the same study area that seed removal of *Q. crispipilis* was higher in the forested than in the open habitats

during the acorn fall period, however during periods of low abundance or zero acorn availability there were no such differences between habitats. Conversely, in this study, spatial differences in removal patterns were detected during the non-masting year, suggesting that complex patterns of abundance and behaviour of different acorn consumers interact with seed availability (Price & Jenkins 1986). Seed abundance may affect the habitat use of small mammals by affecting their population growth (Banks & Dickman 2000) and processes such as inter and intra-specific competition for space (Pusenius *et al.* 2000) and resources (McShea 2000; Kotler *et al.* 2001).

Space use and foraging by small mammals may also be influenced by their risk of predation (Kotler *et al.* 1991; Korpimäki & Krebs 1996; Jonsson *et al.* 2000). The assumption that arboreal rodents may avoid edges because the risk of predation is higher than that of interior habitats was not supported by the results comparing hard edges and adjacent forest interiors, as more acorns were removed, and in a shorter time, near the edge than in the forest interior. Previous studies have reported increased seed predation near the edge than the forest interior (Bonfil & Soberon 1999; Kollmann & Buschor 2002; Jules & Rathcke 2003) or the opposite situation (Burkey 1993; Diaz *et al.* 1999). Other studies have found no difference in seed removal between the edge and forest interior (Notman *et al.* 1996). Bonfil & Soberon (1999) found that acorn removal of *Quercus rugosa* in a dry oak forest in Mexico was higher in the forest border compared with the forest interior and a disturbed shrubland, however they did not test replicated and adjacent habitats. The distance at which the seeds were placed from the edge varies greatly between studies. Some studies placed seeds at large distances, 30-500 m from the edge (Burkey 1993) or 25-250 m (Holl & Lulow 1997), others, as in the present study, tested small-scale differences 1-50 m from the edge (Kollmann & Buschor 2002). The lack of general patterns may therefore be partly the consequence of methodological differences between investigations, as well as variation in the predator's preferences, density, species composition, and habitat selection of small-mammal seed predators (Ostfeld *et al.* 1997).

Seed predation may be higher at the edge due to higher activity of small mammals owing to relatively high seed production along the edges (Ranney *et al.* 1981). Small mammals may also use the edges as corridors, thus increasing the likelihood of incidental predation (Lidicker 1999). In addition, animals living in the forest patches or in the grasslands may penetrate into the neighbouring habitats and their activity in these less-preferred habitats may be concentrated in the edge (Andren & Angelstam 1988; Heske 1995; Lidicker 1999; Horvath *et al.* 2001). It has also been found that squirrels living in the edge may present higher survival rates than in the forest interior. For example, Anderson & Boutin (2002) found during a 12-year study that juveniles of red squirrels (*Tamiasciurus hudsonicus*) living in the forest edge expressed less risky behaviour that forest-interior juveniles; edge juveniles spent more time in the nest, less time travelling, and less time foraging than interior juveniles. They suggest that edge juveniles may have lower energy demands, requiring them to spend less time foraging and less time exposed to predators, and therefore demonstrate higher survival rates than forest interior juveniles.

A high proportion of acorns removed along the edge was also recorded in both edge types when acorns were exposed on the ground accessible only to small mammals and to all predator types (Chapter 3), suggesting that small mammals did not avoid the edge because they perceived a higher predation risk. During the masting year, the presence of partially eaten acorns with teeth marks together with the high proportion of acorns that were damaged *in situ* suggest that squirrels were the main acorn consumers. If squirrels were the major acorn predator during the masting year (when lower population densities of mice were recorded: Chapter 3), their activity was not significantly affected by proximity to the forest edge, contrary to my expectations. However, during the non-masting year, potential acorn consumer identification was not possible as most of the acorns were removed, which may indicate that mice, rather than squirrels discovered the dishes. This may be supported by the fact that mice populations were higher during the second year and semi-arboreal behaviour was directly observed for *Peromyscus* species when captured animals were released from the traps in the capture-recapture study (Chapter 3). If *Peromyscus* species removed most of the acorns during the second year, they did not penetrate into the

forest edge from the adjacent grasslands in sites with hard edges (Chapter 3). The two squirrel species and the semi-arboreal rodents occurring in the study area may have different microhabitat preferences, resulting in the observed spatial differences in acorn removal during the second year.

Sites with soft edges in both years, as predicted, showed no differences in acorn removal regardless of distance from the edge, and showed higher removal at the forest edge (0 m) compared with hard edges (0 m). These results suggest that adjacent land use affected the probability of acorn survival along the edge; in years with low acorn abundance, higher removal or predation may be expected along the soft edges, which may limit oak regeneration. However long-term research must be undertaken to verify the predictability of spatial differences between years with different acorn availability. Differences in adjacent habitat are likely to be accompanied by changes in predator abundance and species composition. For instance, soft edges presented a higher abundance of mice than hard edges (Chapter 3).

Acorn species

The results obtained during the first year of this study partially support those of previous studies, which suggest that small mammals, including squirrels, are able to detect and respond in different ways to acorns with different germination patterns (Smallwood *et al.* 2002). Early germination of *Q. segoviensis* acorns leads to higher consumption and removal compared with the dormant and smaller *Q. laurina* acorns. However, the fact that in the second year (non-mast seeding year) acorns with faster germination and acorns with dormancy were removed equally makes it difficult to separate the effects of acorn size from the effects of acorn perishability on rodent preferences.

Excision of embryos by squirrels as reported in other studies (Steele *et al.* 2001) was not observed in remaining *Q. segoviensis* acorns. Most of the observed cotyledon damage was at the distal end of the acorn, or to one side of the embryo, permitting germination. This could be explained by a high tannin concentration near the

embryo, as has been recorded in some other oak species (Steele *et al.* 1993); however, data on the chemical composition of *Q. segoviensis* acorns are not available.

It should be noted that the experimental design used may have influenced the rates of seed predation recorded because dishes nailed to trees do not represent the natural spatial distribution of the seeds. During the masting year, experimental dishes with acorns appeared to be used as acorn caches. During the masting year partly consumed acorns or husks were found at the end of the experiment. Squirrels did not remove acorns of *Q. laurina* from the dishes and moreover, *Q. laurina* acorns and *Persea americana* seeds were actually brought to and stored in the dishes. If the dish is considered as a cache, results from the first year of the experiment coincide with those of other studies that have indicated that squirrels store dormant acorns rather than early germinating acorns which are a more perishable food resource (Steele *et al.* 2001). The specific cues on which squirrels rely to make such decisions have been studied recently (Steele *et al.* 2002) and suggest that a chemical cue in the shell of acorns is important in the detection of seed dormancy.

During the second year most acorns were removed intact and either consumed elsewhere or stored. Because the second year was a non-masting year it is possible that the dishes were considered unsafe to store acorns, compared with the masting year in which competition for food between seed predators was relatively low. It is likely that predators removed most of the seeds to safe places or consumed them due to low food availability.

Implications of masting in oak recruitment

The results of this study indicate that during masting years the probability of acorn survival is higher than in non-masting years. In years of abundant acorns, masting may result in seed predator satiation with the huge production of acorns exceeding the number of seeds that can be consumed by the total predator complex (Janzen 1971b). Predator satiation and density dependent seed survival have been

extensively studied for many oak species (see review Chapter 3). Jensen (1982) calculated that rodents consumed about 1-10.3% of the *Q. robur* crop in mast years, while in years with lower acorn production this figure ranged from 30 to 100%.

Higher acorn removal in the edge of the forest may represent higher acorn dispersal as a proportion of the cached acorns may survive (Smith & Reinchman 2002). Edges have been considered suitable microsites for oak regeneration because they may provide intermediate conditions of light equivalent to small forest gaps (Crow 1988). If acorns are cached along the edges this may represent a positive effect for oak regeneration. Also small mammals may remove acorns from the edge and cross soft edges and disperse acorns (Chapter 3) to more suitable sites for acorn germination (Chapter 5) and seedling establishment (Chapter 6). However, higher removal near the edge was recorded during the non-masting year (low availability of acorns) and larger small mammal populations (Chapter 3) rapidly removed most of the acorns, therefore it is possible that most of the acorns removed near edges were eaten. According to the acorn perishability hypothesis (Smallwood *et al.* 2002), in this study, acorns of *Q. crassifolia* would be consumed first by small mammals or their embryo would be excised, whereas acorns of *Q. candicans* would be consumed later, resulting in higher probabilities of escape from predation. Steele *et al.* (2001) followed fates of metal-tagged acorns within the forest and found that *Sciurus aureogaster* in central Mexico, excised embryos of 66.7% of cached acorns of *Q. crassifolia* (faster germination) and only 1 % of those acorns of *Q. candicans* (acorns with dormancy).

It has been documented in temperate forests that squirrels exert a significant impact on dispersal and establishment of oaks. Tree squirrels represent potentially significant dispersal agents of acorns with dormancy, but are devastating seed predators of acorns with early germination (Steele *et al.* 2001). Squirrels cache red oak acorns far more often and at further distances from the parent tree than white oak acorns (Smallwood *et al.* 1998). As a consequence, it has been documented that seedlings of red acorns are dispersed greater distances from parental sources, while seedlings of white oaks showed a clumped distribution close to parent trees

(Smallwood *et al.* 1998; Steele & Smallwood 2002). In the Highlands of Chiapas, where several oak species co-occur in the canopy, differences in their regeneration ecology (occurrence of mast seeding years, germination timing, acorn size, tannin concentrations, etc.) may partly explain their coexistence and their different patterns of dominance recorded in various habitats. Therefore small mammal preferences may have important implications in the distribution and abundance of oak species, especially when several oak species coexist and have alternate bearing. The dominance of *Q. laurina* in the forests studied here (Chapter 2) may be the result of their dormant acorns that have more chance of escaping predation by small mammals, especially during the mast-seeding year.

Edge effects in oak regeneration processes such as acorn predation have not been studied in Mexican forests before. Understanding how different edges affect oak regeneration processes is important as the proportion of the forested landscape in close proximity to hard edges is increasing, as a result of human activities. This study provides baseline data and highlights the need to thoroughly investigate how vegetation adjacent to forest may affect the behaviour of acorn consumers within the forest and therefore affect the probabilities of acorn dispersal. The specific patterns of acorn removal caused by acorn predators on different species may have a significant effect on the pattern of oak regeneration at the edges and in the interior of forest patches, particularly with respect to the distribution of seedlings. Further research is needed in tropical montane forests to investigate how landscape features such as edge types affect acorn survival of different species, and how the removal patterns change between years. However, by determining final acorn fate following tagged acorns and controlling predator access to the acorn trials, interpretation of results will permit evaluation of the impact of each acorn consumer type.

CHAPTER 5: Germination of oak tree species across different edge types in the Highlands of Chiapas, Mexico.

ABSTRACT

The purpose of this study was to examine the effect of habitat edges on the probability of acorn germination of three oak species *(Q. crassifolia, Q. rugosa* and *Q. laurina*). I evaluated the effects of edge type (hard and soft), habitat type (grassland, edges and forest), and leaf litter cover (covered or uncovered acorns) on acorn germination, by the experimental establishment of acorns along transects crossing habitat edges. More acorns developed into seedlings in grasslands (38%) than in the forest edge (18%) or the forest interior (15%). In sites with soft edges, a higher number of seedlings emerged from acorns covered by litter compared with acorns planted in the adjacent forest edge and forest interior ($P<0.05$). In sites with hard edges; fewer seedlings emerged in the edge (14%) compared with the adjacent grassland (38%), and the adjacent forest (20%) presented intermediate values. However, in sites with soft edges significant differences in seedling emergence were recorded between the grassland (38%) and the forest (10%), whereas the edge presented intermediate values (23%). The effect of leaf litter cover on acorn germination was only significant in grasslands in sites with soft edges ($P<0.05$). Acorns in grasslands received relatively little insect damage (10%) compared with the edge (19%) and the forest (30%, $P<0.05$), emphasising the importance of acorn dispersal for successful oak establishment. The implications for regeneration of these oak species and the dynamics of montane oak forest in Mexico are discussed.

INTRODUCTION

The genus *Quercus* (oaks) is one of the most important groups of woody plants in many regions of the Northern Hemisphere. Oaks dominate various temperate, subtropical and tropical forest types, and are also a major component of chaparral and scrub vegetation in many areas. The Highlands of central and eastern Mexico are the major centre of diversity for the genus (Nixon 1993) where oak species occur

mostly as evergreen and semi-evergreen trees, either as the sole canopy dominant or in association with pine (González-Espinosa *et al.* 1991; González-Espinosa *et al.* 1995; Galindo-Jaimes *et al.* 2002).

Oaks are almost exclusively dependent on animals as dispersal agents (Steele & Smallwood 2002). Birds and mammals consume acorns during the acorn ripening season, but also cache and hoard most of the remaining acorns in the soil as a future food reserve. As not all of the cached seeds are recovered, caching can contribute to seed dispersal (Howe & Smallwood 1982). The microhabitats where acorns are buried are therefore potentially important for acorn germination and seedling development. Few studies have investigated oak establishment in microhabitats representing the range of acorn dispersal sites (Kollmann & Schill 1996). Sites such as forest edges and grasslands potentially may present more suitable growing conditions for oak seedlings than under the oak canopy where intra-specific competition and higher exposure to predators can reduce seedling growth and survival (Howe *et al.* 1985).

The factors that affect acorn germination within forest stands have been extensively studied over many decades for North American oak species (Barrett 1931; Crow 1988; Borchert *et al.* 1989; Lorimer *et al.* 1994; Ashton & Larson 1996; Fuchs & Krannitz 2000; Garcia *et al.* 2002), Northern Europe species (Watt 1919; Shaw 1968; Kollmann & Schill 1996) and more recently in Mediterranean ecosystems (Espelta *et al.* 1995; Rey-Benayas 1998; Branco *et al.* 2002). However less attention has been given to the study of acorn germination in tropical cloud montane forests (Guariguata & Saenz 2002; Tripathi & Khan 1990; Camacho-Cruz *et al.* 2000).

Germination of acorns has been studied experimentally as a function of factors such as seed burial depth (Borchert *et al.* 1989; Nyandiga & McPherson 1992; Barik *et al.* 1996; Kollmann & Schill 1996; Li & Ma 2003), leaf litter cover (Shaw 1968; Borchert *et al.* 1989; Nyandiga & McPherson 1992; Barik *et al.* 1996; López-Barrera & González-Espinosa 2001), herbaceous cover (Tripathi & Khan 1990; Barik *et al.* 1996; Kollmann & Schill 1996), soil moisture (Ashton & Larson 1996), acorn size or

mass (Tripathi & Khan 1990; Barik *et al.* 1996; Bonfil 1998; Ke & Werger 1999), insect damage (Branco *et al.* 2002), cotyledon removal (Bonfil 1998; Li & Ma 2003) and soil type (Sonesson 1994).

Moisture has been proposed as the main factor explaining variability in acorn germination (Germaine & McPherson 1998; Garcia *et al.* 2002), and therefore it is not surprising that previous studies have emphasised the positive effect on acorn germination of herbaceous ground cover and leaf litter (Li & Ma 2003). Jarvis (1964a) found that the loss of acorn moisture was much less when covered by litter than for those acorns placed on the ground surface, and that water content was related to marked differences in viability and germination (Garcia *et al.* 2002). Bare mineral soil may be unfavourable for acorn germination because of exposure to high temperature and humidity fluctuations (Borchert *et al.* 1989; Fuchs & Krannitz 2000) and high probability of removal by acorn predators and/or dispersers (Shaw 1968; Borchert *et al.* 1989; Fuchs & Krannitz 2000). However many authors suggest that it is the interaction of moisture with other factors such as acorn species, acorn size, insect damage, temperature and other microhabitat factors that determines rates of acorn germination (Borchert *et al.* 1989; Tripathi & Khan 1990; Nyandiga & McPherson 1992; Ashton & Larson 1996)

Previous studies of *Quercus* germination in north temperate regions have documented that acorns of the white oak group (*Leucobalanus*) germinate early in the autumn, whereas acorns of the red oak group (*Erithrobalanus*) present acorn dormancy during the cold winter (Bourdeau 1954). However, in the case of subtropical species there is a lack of information about germination times. In temperate forests, there is evidence to suggest that acorn germination schedules directly affect the foraging behaviour of small mammals: acorns that are close to germination are consumed or partially consumed and stored, whereas dormant acorns tend to be stored by small mammals (Fox 1982; Smallwood *et al.* 2002; Steele *et al.* 2002). Therefore there is a need to document the timing of germination of different neotropical oak species, as this may play an important role in determining acorn dispersal probabilities.

In highland Mexico, oak forests have been highly fragmented as a result of human activity, primarily agriculture (De Jong *et al.* 1999). Processes such as shifting cultivation and tree harvesting result in the creation of forest patches and an increase in the availability of forest edges (Ochoa-Gaona & González-Espinosa 2000). Forest edges produce physical environments that differ from both open areas and forest interiors (Chen *et al.* 1995), and seem to provide a suitable regeneration site for oaks by providing intermediate irradiance and moisture availability. Ranney *et al.* (1981) classified oaks as an edge-orientated group. Gehlhausen *et al.* (2000) found that edges are a refuge for saplings of *Quercus* spp. and he suggested that seedlings of oaks were unable to compete with shade-tolerant species in the forest interior. However, Herlin & Fry (2000) suggested that the occurrence in the edge of *Quercus robur* may be attributable to a favourable environment that attracts animals or facilitates dispersal of plants towards the edge. Despite all the research attention that has focused on oak regeneration, I am unaware of any previous experimental investigation of the effects of different habitat edges on acorn germination.

Previous research (Chapters 3 and 4) has found that acorns display different probabilities of dispersal by rodents into grasslands and within the forest patches, and this is determined among other factors by the edge type. Hard edges create an abrupt change in the light environment at the soil surface, whereas in soft edges there is a gradual change in vegetation cover (Chapters 2 and 3). Previous data describing the microsites where acorns can be dispersed suggest that acorns may be cached then covered by litter. The present study expands this research experimentally by evaluating acorn germination within different microsites within forest, edge, and grassland habitats, including different edge types and presence or absence of litter covering the acorn. The general hypothesis is that, as environmental variables such as light and humidity change abruptly across hard edges, similarly, will cause marked changes in acorn germination either side of the edge. However this effect will be less pronounced across soft edges. Specific hypotheses are that germination rate will be higher in acorns covered with leaf litter or matted grass roots and faster in acorns of white oaks compared to acorns of red oaks.

METHODS

Acorns

Acorns were collected from the forest floor from October 2000 to January 2001. Acorns of each species were collected from the vicinity of separate parent trees located in the study area (*Q. laurina* and *Q. crassifolia* in Rancho Merced Bazom) and nearby areas *(Q. candicans* in Estacion Biologica Huitepec and *Q. rugosa* in Mitziton). After collection acorns were stored within paper bags in a refrigerator (5º C) until the start of each experiment. An equal number of acorns for each parent source were mixed together for each species. Viability was tested by floating acorns in water, which is a reliable method to identify insect-damaged acorns (Gribko & Jones 1995); only those acorns that sank were subsequently used in germination trials. Acorn characteristics (diameter, fresh and dry mass) of a random sample of 100 acorns from each oak species were measured at the beginning of the experiments. The main characteristics of the acorns used in this study are summarised in Table 5.1. All the species used in this study may occur together as canopy trees in the Highlands of Chiapas.

Table 5.1 Main acorn characteristics. Acorn moisture was estimated only for the species included in the field experiment. Reported values are means ± 1 SE, (n=100).

Species	Subgenus	Acorn diameter (cm)	Acorn mass (g)	Acorn moisture (%)
Q. candicans	*Erithrobalanus*	2.01±0.02	4.51±0.09	-
Q. crassifolia	*Erithrobalanus*	1.33±0.02	1.99±0.05	18.33±2.14
Q. laurina	*Erithrobalanus*	1.35±0.02	1.80±0.06	31.63±0.79
Q. rugosa	*Leucobalanus*	1.45±0.03	2.94±0.08	36.68±0.63

Laboratory trials

In February 2001 an experiment was set up in a laboratory under indoor daylight conditions (33.3 ± 1.3 μmol m^{-2} s^{-1}, measured during daylight hours). Mean temperature in the laboratory was 16.7 ± 2.9 º C (mean ± SD; minimum and mean

maximum temperatures were 13.4 ± 2.7 and 24.1 ± 4.0 º C). This experiment was designed to identify germination rates and total germination of different oak species under controlled conditions. The date of sowing coincided with the natural seed fall period for these species. Fifty acorns of four species (*Q. laurina, Q. rugosa, Q. candicans* and *Q. crassifolia*) were placed on filter paper within rectangular (25 x 15 x 3 cm) polystyrene foam trays (five trays per species) and covered with filter paper (250 acorns per species). Filter papers within each tray were kept humid (trays were watered every day). Filter papers were changed every week to avoid fungal infection. The position of the trays was randomly changed every third day. Acorns were considered to have germinated when the radicle was visible (>2-3 mm). Germinating seeds were counted every third day and removed from the trays. The experiment was terminated after 217 days, when no further germination was recorded.

Field experiment

To determine whether acorns would germinate if dispersed into grasslands, germination success was monitored in a field experiment. In April 2001 a four factorial experiment (edge type x habitat x planting treatment x species) was set up. For details of the study area see Chapter 2. According to weather records supplied by the National Water Commission, in the study area the mean maximum and the mean minimum temperature from April to June 2001 were 22.1 ± 0.6 (± SD) °C and 7.8 ± 1.8 °C. Total rainfall per month for April, May and June was 76.3, 190.4 and 108.1 mm, respectively. A detailed description of the study area is available in Chapter 2. For the purposes of this study, six sites with grasslands and adjacent pine-oak forest (three sites with hard edges and three sites with soft edges) were chosen (details of the experimental plots are presented in Chapters 2 and 3).

The experiment was set up within the experimental fenced plots. Habitats contrasted consisted of grassland (a transect parallel to the edge, 24 m from the edge), forest edge and forest interior (a transect parallel to the edge, 24 m from the edge, inside the forest patch). Information about vegetation structure and composition in each habitat is presented in Chapters 2 and 3. Planting treatment consisted of an acorn

placed below different covering material (2-3 cm of leaf litter, grass, grass roots or soil depending on the microhabitat) and uncovered control acorns, just placed on the soil surface. Acorns of *Q. laurina, Q. rugosa* and *Q. crassifolia* were tested, *Q. candicans* were not included in this experiment because of the lack of acorns.

Wire enclosure cages (50 x 50 x 15 cm, mesh size 1 cm^2) were erected around each of the experimental trials to prevent acorn predation. The cages were buried (to a depth of 7-8 cm) and fixed with spikes. Planting treatment was randomly assigned to each cage. Paired cages (one cage with acorns covered and the contiguous cage with uncovered acorns) were randomly located within each habitat treatment. Each cage was imaginarily divided into four sub-quadrats (25 x 25 cm) within which the three species of acorns were randomly located (one sub-quadrat remained empty). In each quadrat 20 acorns per species were planted at a distance of 5 cm apart in a 5 x 4 grid. The experiment was terminated after 73 days and all acorns (except those acorns that produced seedlings) were removed and analysed in the laboratory. Non-germinating acorns were opened to determine the possible cause of death. After analysis of their fate, acorns of each species from each cage (planting treatment) were pooled and their fresh mass was obtained. Acorn moisture proportion at the end of the experiment was obtained by oven drying within paper bags at 70 º C for 72 hr until constant mass was reached, and their water proportion was calculated by the difference in mass (gravimetric method) before and after drying the samples (fresh mass - dry mass). Moisture content is expressed on a fresh weight basis.

Micro-environmental variables were measured every 20 days from the beginning of the experiment. Soil moisture content was estimated from cylindrical samples (18 cm^3) taken from each paired cage at a depth of 4 cm within mineral soil. Moisture content was obtained by the gravimetric method. Photosynthetically active radiation (PAR μmol m^{-2} s^{-1}) reaching the soil surface (10 cm above the soil) in the centre of each paired cage was estimated using a ceptometer (Sunfleck Decagon Pullman, Washington, USA).

Statistical analysis

Percentage germination at the end of the experiments (number of acorns germinated / total number of acorns) was not normally distributed and therefore data were transformed by obtaining the square root of the proportion and then the arcsine (Sokal & Rohlf 1998). One-way ANOVA was used to analyse the effect of species in the laboratory trial (SPSS v.10.0.1). Because acorn germination percentages obtained in the laboratory experiment were near 100%, means and asymmetric confidence intervals were back transformed from radians. The shape of the curves of cumulative proportion of germinated acorns over time was compared with a survival function using the log-rank statistic and pairwise comparisons (Kaplan Meier procedure, SPSS v.10.0.1).

Germination (defined as acorns with radicles ≥ 2 mm long) at the end of the field experiment was tested in a crossed ANOVA model including all their possible interactions (SPSS v.10.0.1). Experimental factors were edge type, habitat, treatment cover and species. As a second analysis, acorns were classified in each of the following categories: 1) intact radicle, 2) insect damaged radicle, 3) developed into plumules (stem of 5-10 cm with no leaves), 3) developed into seedlings (≥ 2 leaves), 4) non-germinated rotten acorns, 5) non-germinated acorns, but apparently viable and 6) non-germinated acorns with insect damage. Proportions (transformed using the arcsine transformation) of acorns in each category were analysed as a function of the experimental factors using MANOVA and one-way ANOVA (SPSS v.10.0.1).

Soil moisture (arcsine transformed) and PAR reaching the soil surface ($\log_{10}$ transformed) in each paired cage were analysed using ANOVA and testing the effect of edge type (hard and soft) and habitat (grassland, edge and forest). Tukey's HSD multiple comparisons were used to detect significant differences among treatment means (SPSS v.10.0.1). All full ANOVA and MANOVA tables are presented in Appendix 4 (Tables A.4.1-A.4.7) in the same order as they were reported in the results section. In the text, means are given ± 1 SE unless otherwise stated.

RESULTS

Laboratory trials

After 217 days, the final proportion of acorns that germinated varied significantly between species ($F = 40.17$; df=3, 12; $P<0.001$). *Q. laurina* and *Q. rugosa* acorns showed the highest values (99.7%, confidence intervals: 97.6-99.8% and 99.5%, 96.5-99.7%, respectively), *Q. candicans* acorns showed an intermediate value (86.5%, 77.5-93.5%) and the lowest value was found for *Q. crassifolia* acorns (74.1%, 67.8-79.9%).

Shapes of germination curves through time (Fig. 5.1) were significantly different between all species (Log-rank = 115.97; df = 3; $P<0.001$). Germination occurred first in acorns from *Q. crassifolia* (7 days after placement) followed by *Q. rugosa* (14 days), *Q. candicans* (21 days) and *Q. laurina* acorns (35 days). Constant values of germination were recorded for *Q. rugosa, Q. crassifolia* and *Q. candicans* after 91 days of the experiment, while *Q. laurina* acorns reached constant values after 203 days from the beginning of the experiment.

Acorn germination in the field

Total germination in the field was significantly affected by the interaction of edge type, habitat and cover (Table 5.2). Therefore, consideration of main effects is not appropriate and interpretation is based on interaction means. The positive effect of covering the acorns with litter or grasses on acorn germination was more evident in the grasslands, but only in those sites with soft edges (Fig. 5.2). Germination was also affected by the interaction of habitat and species (Table 5.2). Differences between the three species were more evident in the forest edge; the highest germination was for *Q. rugosa* acorns and the lowest for *Q. crassifolia* (Fig. 5.3).

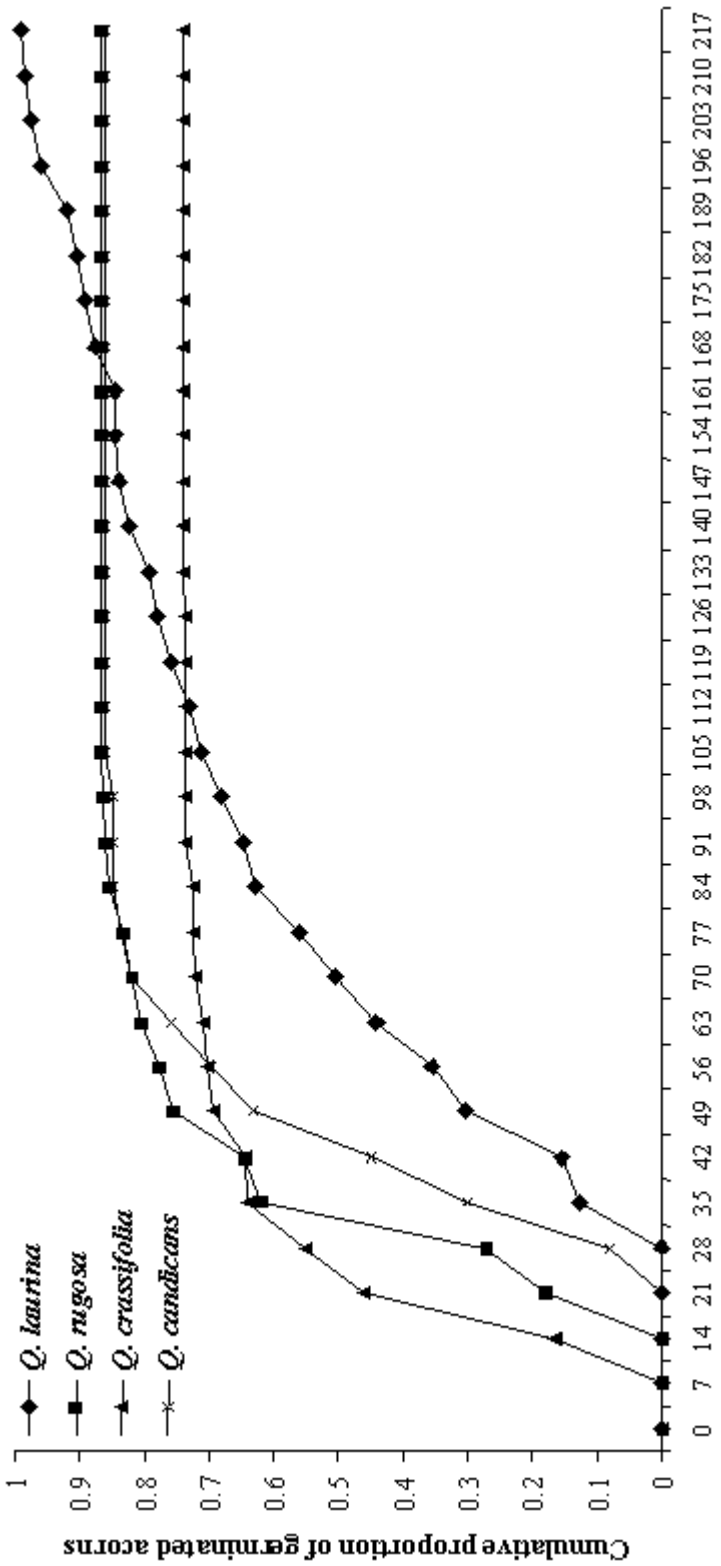

Fig. 5.1 Cumulative proportion of germinated acorns of four species under laboratory conditions from February to October 2001. The overall shapes of the species curves were all significantly different from one another as determined by the log-rank comparisons (P<0.05).

Table 5.2 ANOVA of the influence of experimental factors: edge type (hard and soft), habitat (grassland, edge and forest), cover (covered and uncovered acorns) and species (*Q. laurina, Q. rugosa* and *Q. crassifolia*) on the proportion of germinated acorns.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.366	0.366	6.19	0.015
Habitat	2	0.044	0.022	0.37	0.693
Cover	1	0.931	0.931	15.74	0.000
Species	2	6.245	3.121	52.77	0.000
Edge type x Habitat	2	0.133	0.066	1.12	0.331
Edge type x Cover	1	0.048	0.048	0.81	0.371
Edge type x Species	2	0.252	0.126	2.13	0.126
Habitat x Cover	2	0.647	0.323	5.47	0.006
Habitat x Species	4	0.673	0.168	2.84	0.030
Cover x Species	2	0.206	0.103	1.74	0.183
Edge type x Habitat x Cover	2	0.743	0.371	6.28	0.003
Edge type x Habitat x Species	4	0.307	0.077	1.30	0.279
Edge type x Cover x Species	2	0.144	0.073	1.22	0.302
Habitat x Cover x Species	4	0.262	0.065	1.11	0.360
Edge type x Habitat x Cover x Species	4	0.220	0.055	0.93	0.452
Error	72	4.259	0.059		

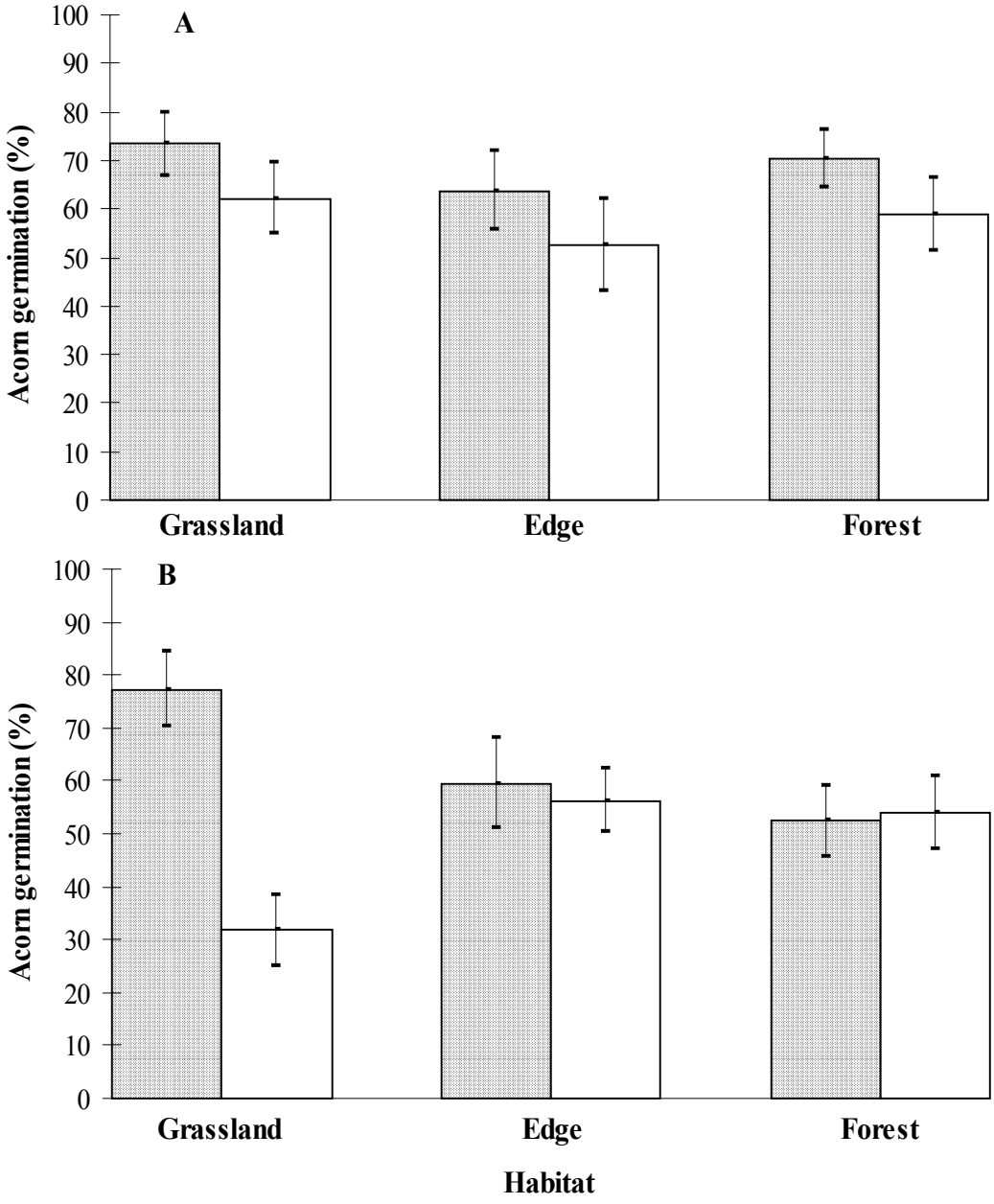

Fig. 5.2 Percentage of acorn germination (mean ± 1 SE) under different edge types: A) hard and B) soft, habitat types, and planting cover treatments: covered acorns (shaded bars) and uncovered acorns (open bars). Data for all the species combined.

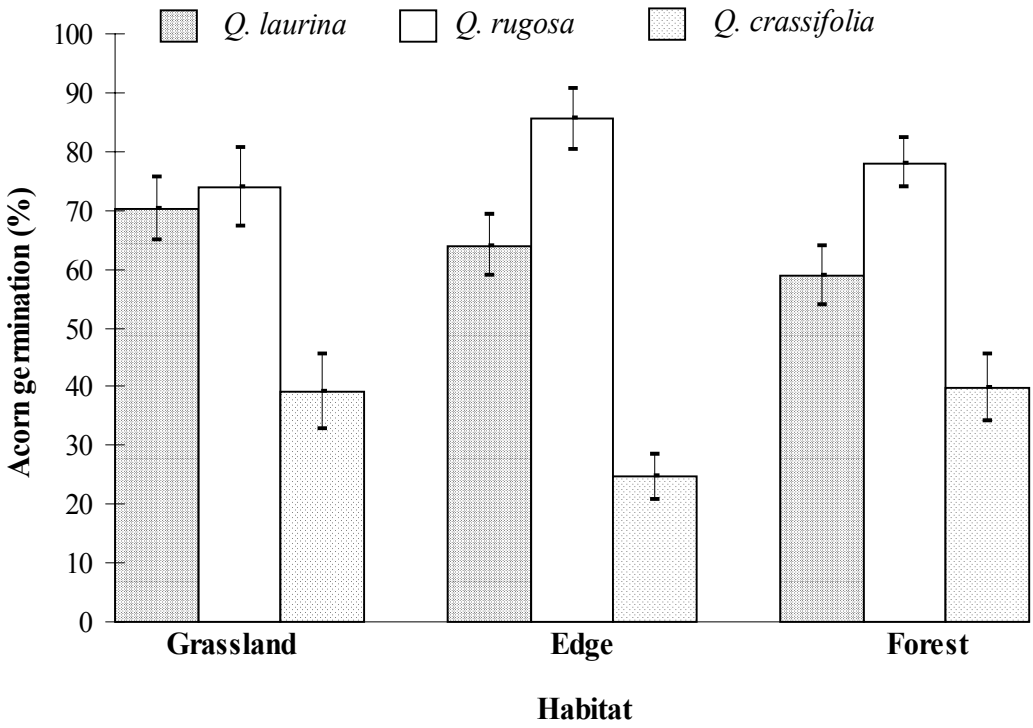

Fig. 5.3 Percentage of germination (mean ± 1 SE) of *Q. laurina, Q. rugosa* and *Q. crassifolia* under different habitat types.

Acorn fate

At the end of the experiment, there were significant main effects of species (MANOVA, F=9.50; df=14, 134; P<0.001), habitat (MANOVA, F=3.58; df=14, 134; P<0.001), cover (MANOVA, F=5.18; df=7, 166; P<0.001) and the interaction between edge type and habitat (MANOVA, F=2.45; df=14, 134; P=0.004) and the interaction between habitat, cover and species (MANOVA, F=1.82; df=28, 276; P=0.008), with different univariate effects on the final fate of the acorns. There were significant differences among species in the proportion of acorns that were rotten, viable and the proportion of acorns that developed plumules and seedlings (Table 5.3). Ungerminated acorns of *Q. crassifolia* were mostly rotten or had insect damage; a small fraction was apparently viable. Although germination and seedling emergence of *Q. rugosa* was higher than *Q. laurina*, analysis of ungerminated acorns showed that a high proportion of *Q. laurina* acorns were apparently viable and may have had the potential to germinate after the experiment ended (Table 5.3).

A higher proportion of acorns produced seedlings when acorns were planted covered by litter or grasses in the grasslands than in the other habitat types (F=5.06; df=2, 72; P=0.009, Fig. 5.4). The proportion of germinated acorns that had insect damage (family *Curculionidae*) was higher within the forest, decreasing in the edge and in the grassland (Table 5.3).

Table 5.3 Fate of acorns (mean percentage ± 1 SE) at the end of the study period (73 days) as a function of the main experimental factors. Asterisks in the columns represent the range of the P value of the main effects determined by MANOVA and univariate ANOVAS. Means followed by the same letter are not significantly different for the main treatment and species effects as determined by Tukey's test * = ($P \leq 0.05$), ** = ($P \leq 0.01$), *** = ($P \leq 0.001$).

	Germinated				**Non-germinated**		
	Radicle	**Insect damaged**	**Plumules**	**Seedlings**	**Rotten**	**Viable**	**Insect damaged**
Edge type							
Hard	18.3±2.4	14.4±2.6	10.9±1.5	24.2±2.9	16.1±2.7	8.7±1.9	7.3±1.3
Soft	24.5±2.4	6.8±1.4	10.3±1.2	23.2±3.1	17.8 ± 3.3	6.7±1.4	10.7±2.2
Habitat							
Grassland	26.0±3.5a	4.2±1.5a	8.7±1.4	38.0±4.5a	12.4±3.2a	4.6±1.3	6.1±2.1a
Edge	20.3±2.5ab	10.1±2.8ab	12.5±1.9	18.4±2.7b	19.2±4.3b	10.9±2.7	8.5±1.9ab
Forest	17.9±2.9b	17.4±2.9b	10.6±1.7	15.1±2.4b	19.2±3.6b	7.5±1.7	12.3±2.4b
	*	***		***	**		*
Species							
Q. laurina	20.8±2.5	11.8±2.5	11.7±1.5a	28.1±3.9a	7.4±1.5a	13.2±2.4a	7.0±2.0
Q. rugosa	23.5±2.1	12.7±3.3	14.3±1.9a	33.2±3.2a	3.5±0.7a	4.5±1.5b	8.3±2.1
Q. crassifolia	19.7±4.1	7.4±1.9	5.7±1.3b	9.4±2.6b	40.7±4.0b	5.4±1.7b	11.7±2.5
			***	***	***	***	
Planting							
Covered	19.1±2.1	10.6±2.2	12.5±1.5	26.7±3 .4	19.8±3.3	3.7±0.7	7.5±1.7
Uncovered	23.7±2.7	10.6±2.1	8.7± 1.2	20.6±2.5	14.1±2.6	11.8±2.1	10.4±1.9
			*		*	***	

There was a significant interaction between edge type and habitat in the proportion of seedlings that emerged (F=4.59; df=2, 72; P=0.013). In sites with soft edges, more acorns developed into seedlings when they were planted in the grasslands compared with the adjacent forest and the edge, whereas the edge presented intermediate values (Table 5.4). In sites with hard edges the response was different, higher number of seedlings emerged when acorns were planted in the grasslands compared with the

edge, and within the forest seedling emergence presented intermediate values (Table 5.4).

The mean acorn moisture content at the end of the experiment followed the same patterns that the mean soil moisture measured in each habitat and edge type (Table 5.4). Mean soil moisture along the experiment (April, May and June 2001) was not significantly different between habitats or edge types (ANOVA, $P>0.05$, Table 5.4). The PAR reaching the soil surface was affected by the habitat type ($F=78.82$; df=2, 18; $P<0.001$), grasslands displaying the highest value (630.5 ± 57.5 μmol m^{-2} s^{-1}), forest edge an intermediate value (54.2 ± 9.7 μmol m^{-2} s^{-1}) and forest interior the lowest (15.6 ± 2.7 μmol m^{-2} s^{-1}).

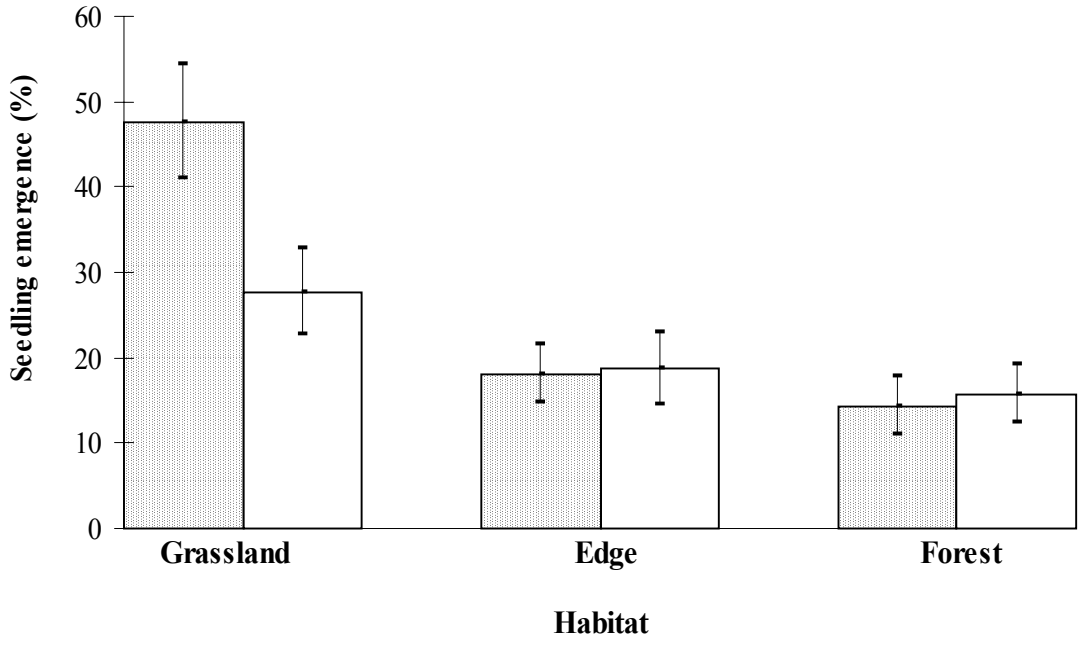

Fig. 5.4 Percentage of seedling emergence (mean ± 1 SE) under different habitats and planting cover treatments: covered acorns (shaded bars) and uncovered acorns (open bars). Data for all the species combined.

Table 5.4 Means (± 1 SE) of light (PAR) and soil humidity during the study period associated with acorn moisture and the final fate of acorns (mean percentage ± 1 SE) at the end of the experiment (73 days), as a function of edge type and habitat. Percentages represent the proportion of the total number of acorns tested (20 acorns per species per treatment combination). Means followed by the same letter are not significantly different as determined by Tukey's test ($P<0.05$).

					Germinated				Non- germinated		
Edge Type	**Habitat**	**Soil humidity** (%)	**PAR** (μmol m^{-2} s^{-1})	**Acorn moisture** (%)	**Radicle** (%)	**Insect damaged** (%)	**Plumules** (%)	**Seedlings** (%)	**Viable** (%)	**Rotten** (%)	**Insect damaged** (%)
Hard	**Grassland**	11.8±0.4	721.5± 88.1	29.6±1.2	19.6±3.5	7.0± 2.7	9.0±2.0	38.2±5.9**a**	7.4±2.2	16.1±4.9**a**	2.7±1.5
	Edge	12.5±0.4	58.3±12.3	33.2±0.6	20.8±4.3	13.3±5.0	14.0±3.5	14.0±3.2**b**	11.8±4.2	17.1±5.3**a**	9.1±2.9
	Forest	13.9±0.9	15.1±5.1	35.8± 0.5	14.5±4.8	22.8±4.7	9.7±2.2	20.5±3.9**ba**	7.1±3.0	15.1±4.3**a**	10.3±2.2
Soft	**Grassland**	13.6±0.9	539.6±59.2	30.7±0.9	32.9±5.9	1.3±0.7	8.4±2.1	37.7±7.0**a**	1.7±0.9	8.4±4.0**a**	9.6±4.0
	Edge	14.6±1.3	50.1±16.0	34.0±0.4	19.8±2.6	6.8±2.2	11.0±1.8	23.0±4.0**ab**	10.1±3.4	21.4±6.9**b**	7.9±2.6
	Forest	12.7±0.6	16.0±2.4	35.3±0.4	21.3±3.3	12.0±3.0	11.4±2.6	9.7±2.1**b**	9.0±1.7	23.3±5.6**b**	14.3±4.4

DISCUSSION

Edge type and habitat effects

Results of this study showed that germination and seedling emergence generally were higher in the grasslands than in the forested portion of the site, but the optimal response in acorn germination differed among edge types and planting treatments.

In this experiment, habitat type had a greater influence than edge type in determining acorn germination and seedling emergence. The expected changes in soil humidity and acorn germination in the edge and in the grasslands as a function of edge types were not recorded. In general, microsites in the grasslands under a cover of leaf or root litter were more suitable for acorn germination and seedling emergence. Acorns in such sites were less susceptible to rot and were protected from humidity and temperature fluctuations. Additionally, germinated and non-germinated acorns planted in the grasslands presented less insect damage compared with intermediate values recorded in the edge and highest values recorded in the forest. This finding has important implications in terms of the escape hypothesis (Janzen 1971a; Connell 1971). According to the Janzen-Connell hypothesis, seeds or seedlings may be vulnerable if they are located in the vicinity of their parents; seeds that are dispersed may have a survival advantage because they escape attack by their natural enemies. Howe *et al.* (1985) found that 99% of the seeds of *Virola surinamensis* dropped directly under the crown die, mainly as a result of insect predation, whereas those moved to a distance of 45 m were up to 44 times more likely to survive.

In this study, the intermediate values of insect damage recorded in the edge may indicate that there is a positive distance-dependent survival mechanism (Packer & Clay 2000) that underlines the advantages of acorn dispersal. Previous research (Chapter 3) documented that small mammals tend to store single acorns covered by a litter layer (4.2 ± 2.6 cm, ± SD) in grasslands in hard edges (up to 5 m from the edge) and in soft edges (up to 15 m from the edge). In the present work, I found that acorns

placed in the grasslands have higher germination probabilities compared with acorns that are not dispersed and remain under the oak canopy.

The effects of insects on acorn germination and subsequent survival of the seedling are somewhat controversial. It has been suggested that acorns attacked by insects are able to germinate because larval feeding activity is concentrated in the endosperm and seldom results in injury to the embryo (Branco *et al.* 2002), which has been attributed to chemical defence as the plants allocate more tannins in the area of the embryo (Steele *et al.* 1998; Smallwood *et al.* 2002). Barret (1931) found that about 40% of acorns attached to well-developed seedlings had been damaged by insects. There is evidence that insect-attacked acorns have higher (near 90%) germination rates (Branco *et al.* 2002), however seedlings resulting from these acorns exhibited lower survival, slower growth rates and lower dry mass production than non attacked seedlings (Branco *et al.* 2002). Several multi-trophic interactions have been documented between oaks, insects and jays (Hubbard & McPherson 1997) and between oaks, insects and small mammals (Crawley & Long 1995; Steele *et al.* 1996).

Total acorn germination was not significantly affected by the interaction between edge type and habitat, as was hypothesised. However, according to my expectations, spatial variation in seedling emergence was less pronounced in the sites with soft edges than in the sites with hard edges. Higher fluctuations of microenvironmental variables in hard edges may have delayed seedling emergence compared with soft edges. In soft edges the cover given by the adjacent abandoned grassland may provide a partial shade that protected acorns from humidity and temperature fluctuations. The potential benefits of partial shade provided by different habitats (such as pinelands, gaps, shrublands or edges) are complicated by indirect and direct effects on microenvironments that affect acorn germination and seedling emergence (Li & Ma 2003). Callaway (1992) reported that germination of *Q. douglassi* and *Q. lobata* was not different between open grasslands and shrublands, however shoot survival was higher under shrubs. Similarly, Camacho-Cruz *et al.* (2000) found that germination of *Q. laurina* was similar between old-growth forest (87% canopy

cover) and pine-dominated stands (53% canopy cover), however seedling survival was higher in the pine forest. In general, intermediate shade may facilitate seeds and seedlings by reducing the temperature and humidity fluctuations (Bonfil & Soberon 1999) but permitting sufficient light transmission for seedling growth (Crow 1988; Ashton & Larson 1996) and providing protection from large herbivores (Ramírez-Marcial *et al.* 1996).

Measurements of microclimate in the study area recorded that the mean fluctuation between maximum and minimum temperatures and relative humidity in open grasslands were 22.0 ± 9.9 °C and 87.0 ± 6.5%, respectively, whereas within the forest respective values were 2.2 ± 2.1 °C and 60.5 ± 12.2% (Romero-Najera 2000). Surprisingly, acorns exposed to these contrasting environmental conditions displayed similar germination rates. The most probable explanation for these results relates to the characteristics of the seedbed structure present in the grasslands. In the open grasslands in hard edges, intensive grazing maintained a homogeneous and interwoven layer of grass stems and roots where even acorns planted on the surface move downwards and became covered by grasses. This thinner cover was enough to provide a moist environment and protected acorns from temperature and humidity fluctuations. On the other hand, in the grasslands of soft edges the patchy shrub or tall herbaceous strata provided enough shade to inhibit the formation of a continuous prostrate and dense herbaceous layer. This results in a highly heterogeneous microsite with a higher proportion of bare soil; acorns sowed uncovered remained on the surface, and consequently were more exposed to desiccation. This explain the presence of fewer rotten acorns and more seedlings emerging when acorns were covered by litter in these habitats, suggesting that in abandoned grasslands (with heterogeneous vegetation cover) the presence of additional leaf litter cover determined acorn moisture and successful acorn germination.

Moisture content of the remaining acorns at the end of the experiment did not reflect these differences between habitats. However, it should be noted that the appearance of acorns may not accurately reflect the cause of mortality (Watt 1919). For example acorns that have previously dried may present broken husks that may enhance water

absorption, rottenness, fungal attack or insect damage. Acorns at the end of the experiment were characterised by a relatively high moisture content (30-35% expressed as the proportion of the fresh mass): for comparison, values of 40% (Branco *et al.* 2002) and 50% (Garcia *et al.* 2002) have been reported for fresh and intact acorns. Therefore the data presented here describing the final condition of the acorns should be interpreted with caution.

Species-specific differences in germination

Results of this study indicate that the *Quercus* species tested responded differently to microhabitat characteristics and displayed different germination timings. I expected more rapid germination of *Q. rugosa* acorns (white oak) and dormancy of *Quercus* species belonging to the red oaks group. However, all four species displayed different germination timings and acorns of *Q. crassifolia* (red oak) germinated earlier than *Q. rugosa*. This may indicate that some oak species can be considered as intermediate (possessing ecological characteristics of both subgenera). Earlier germination could be correlated with the moderate rainfall present during the winter in the study area (Chapter 2). Differences in timing of germination resulting in differences in acorn perishability may directly affect the behaviour of acorn consumers (Smallwood *et al.* 2002), furthermore, the timing of germination in oaks has been considered as a dispersal syndrome (Steele & Smallwood 2002). Squirrels and other small mammals disperse viable red oak acorns further than they do white oak acorns (Steele & Smallwood 1994; Smallwood *et al.* 1998). Steele *et al.* (2001) found that *Sciurus aureogaster* from central Mexico frequently cached and excised the embryos of acorns that had earlier germination (white oaks), whereas this squirrel species only excised embryos of acorns of the red oaks while they were germinating. Based on these results, it could be hypothesised that the delayed germination of *Q. laurina* (the dominant species in the studied forest, see Chapter 2) may represent an advantage over the other species because it would increase the probability of being cached intact and dispersed longer distances. However, further research in the study area in needed to explore all the implications of the different germination schedules of these coexisting species.

The relatively low germination of *Q. crassifolia* acorns (34%) in the field experiment compared with the potential germination as determined in the laboratory trials (74%) may be the direct result of storing the acorns to be used in the field experiment for two months (at 5 °C) prior to their being planted. Obviously, some factors under field conditions are less optimal for germination than in the laboratory, however the magnitude of this difference was not recorded in *Q. laurina* and *Q. rugosa*. The loss of viability may indicate that acorns of *Q. crassifolia* are difficult to store, whereas other species such as *Q. laurina* can be stored up to one year (pers. obs) without significant loss of viability. A more likely explanation is that acorns of *Q. crassifolia* normally germinate immediately after falling on the forest floor and the husks may present higher water permeability, therefore the embryo may be more sensitive to rot, drought and temperature fluctuations. This is supported by the lower acorn moisture of *Q. crassifolia* at the beginning of the field experiment (14-19% less moisture than the other two species). Acorn moisture less than 30% has been considered lethal to *Quercus* species (Nyandiga & McPherson 1992). It is difficult to conclude whether the tendency of *Q. crassifolia* acorns towards rottenness is a result of the storage or a specific response to the microhabitats. However, the laboratory trials indicate that recently collected *Q. crassifolia* acorns present lower values of germination than the other species tested.

Importance of vegetation cover on acorn germination

The results of this study support those of other studies indicating that leaf litter cover or herbaceous cover can have a positive effect on acorn germination. The litter or mass of grass roots that forms a layer about 2.5-3 cm above the acorns, used in this study, seems to be near the optimal cover thickness as suggested by other studies: 2.5-5 cm for *Q. montana* (Barrett 1931) and 3 cm *for Q. liaotungensis* (Li & Ma 2003). The germination of *Q. laurina* was improved by 15% when acorns were covered by 3 cm deep litter on ground surface (Camacho-Cruz *et al.* 2000). Presence of leaf litter can affect acorn germination by altering insulation, soil temperature, pH, and by changing the availability of moisture (Jarvis 1964; Ahlgren & Ahlgren 1981).

In this study, the effect of litter cover depended on the habitat type. Similar findings were reported by Garcia *et al.* (2002), who reported that under moist substrates, the litter cover effect was not significant on *Q. rubra* germination. However, under conditions of low water availability, acorns covered by a protective layer of leaves suffered lower water losses and displayed higher germination. In this study, observations in the forest edge and within the forest suggested that acorns sowed on a seedbed of oak leaves usually moved downwards and remained covered by one or several layers of leaves. This was also documented in previous detailed studies about litter types (López-Barrera & González-Espinosa 2001). Shaw (1968) found that acorns planted on the surface of oak leaves presented higher germination than those acorns that were buried. He suggested that high air humidity prevented acorn moisture falling to a lethal level. According to this study, additional leaf litter cover may not be important when there is a moist environment (such as in the forest interior) and a seedbed composed of a thick, loose, and heterogeneous layer of relatively large oak leaves that allows acorns to become covered by leaves.

The positive influence of acorn burial in mineral soil on germination rates has been documented in previous studies (Shaw 1968). In a study of Ovington & MacRae (1960), 80% of the acorns of *Q. petraea* that were planted 2.5-3 cm deep germinated, whereas only 1% of the acorns left on the soil surface produce seedlings, because of root desiccation (seed predators excluded). Burial and cover litter also protect acorns against predation of deer (Garcia *et al.* 2002) and small mammals (Borchert *et al.* 1989) by decreasing encounter probabilities.

Despite the positive effects of litter, a negative effect was also recorded in this study for one species. *Q. crassifolia* acorns apparently displayed a higher incidence of rot when acorns were covered by litter and placed in the edge habitat, compared with the uncovered acorns, whereas in the same habitat edges *Q. rugosa* acorns covered by litter developed a higher number of plumules than uncovered acorns. This suggests that the effects of cover can be species specific. These different responses were unexpected, but acorns of *Q. crassifolia* (with relatively rapid germination) may be

more susceptible to excessive moisture availability than other species by presenting a thinner pericarp.

Regeneration implications

This study linked to the previous research investigating acorn dispersal suggests a beneficial effect of small mammals as seed dispersers on oak regeneration. In this sense, acorn dispersers such as *Peromyscus* spp. and blue jays are known to selectively move acorns into early successional areas (as abandoned grasslands, see chapter 3) and forests edges, and to store these acorns by covering them with litter or grass roots (Darley-Hill & Johnson 1981; Kollmann & Schill 1996; Johnson *et al.* 1997). Caching in these open areas under these conditions would match the germination requirements and will facilitate acorn escape from further insect attack.

Results of this study indicated that in general forest edges did not represent the best sites for acorn germination as was expected. However, the fact that more seedlings emerged in soft edges (23%) than in hard edges (14%) emphasises the importance of considering the effect of the edge structure on regeneration processes. Additionally, differences between *Q. rugosa* and *Q. crassifolia* were more pronounced when acorns were covered in the edge habitat, indicating that the edges may evoke species-specific responses. Forest edge moisture availabilities, especially in those sites with soft edges, were similar or even higher than conditions in the forest interior. However forest edges presented intermediate values in the proportion of insect damaged acorns, resulting in an advantage over the acorns fallen within the forest stands.

This study provided empirical information about the species-specific requirements and timing of germination of coexisting species. Overlapping of the germination schedules for the tested species was not recorded, and *Q. crassifolia* was more affected by storage and excessive moisture. Acorn germination patterns of these oak species may provide only a partial explanation for their coexistence, however this

information linked to seedling survival may provide possible mechanisms that maintain oak tree diversity in the study area.

The practical implications of these results for grassland restoration suggest that acorns protected from small mammals can be introduced at the beginning of the rainy season; these should be buried at depth to cover them with the leaf litter or mats of grass roots. If the microhabitat is characterised by the presence of bare soil, it would be necessary to cover the acorns with a 3 cm layer of leaf litter to ensure establishment.

CHAPTER 6: Seedling establishment of five oak species across different edge types and a forest-edge-grassland gradient in the Highlands of Chiapas, Mexico.

ABSTRACT

Previous research in forest-edge-grassland gradients in the highlands of Chiapas, (Chapter 3) has found that acorns have different probabilities of being dispersed by rodents into the grasslands, determined by the edge type. Once acorns are moved into the open sites they are able to germinate (Chapter 5). The present study expands this research by determining experimentally the growth and survival of seedlings of five species (*Q. candicans, Q. crassifolia, Q. laurina, Q. rugosa* and *Q. segoviensis*) across the forest-edge-interior gradient for two edge types (hard and soft). Only *Q. crassifolia* showed significant effects of distance from the edge on seedling survival. Seedling survival and growth was generally higher in the grasslands (plants with higher increases in basal area, higher production of new stems, higher production of new leaves and less defoliation) than in the forested portion of the sites, but the spatial position of optimal seedling performance differed among edge types and species. Overall, *Q. rugosa* presented the highest growth rates and survival across the forest-edge-grassland gradient. The implications of these results are discussed with respect to the regeneration of *Quercus* species in grasslands adjacent to forest fragments, and the role of edge type in determining patterns of colonisation.

INTRODUCTION

For many decades, research in temperate forests has shown that natural regeneration of oak is often limited beneath forest canopies dominated by oaks or other broad-leaved species (Watt 1919). This has been mainly attributed to a) high acorn predation by insects, mammals and birds (Borchert *et al.* 1989; Gomez *et al.* 2003), b) low light availability (Lorimer *et al.* 1994; Thadani & Ashton 1995), c) herbivore damage (Crawley & Long 1995; Ida & Nakagoshi 1996; Wada *et al.* 2000) and d) fungal attack (Crow 1988; Robin *et al.* 2001). Previous studies have suggested that

leaf herbivory by animals and insects can act as the main factor limiting early seedling establishment (Dunning *et al.* 2003; Gomez *et al.* 2003; Riley & Jones 2003). Oak seedlings usually undergo repeated defoliation that may lead eventually to seedling death, particularly when additional environmental stresses such as low light availability, excessive moisture or drought occur (Crow 1988; Riley & Jones 2003). Increased levels of seedling defoliation have been found when seedlings grow directly below the oak canopy (Humphrey & Swaine 1997; Wada *et al.* 2000). However, no attempt has been made to examine the extent of seedling defoliation when seedlings are grown along the habitats that represent their potential dispersal range, including forest edges and adjacent grasslands.

An important factor determining successfully oak establishment seems to be the partial shade provided by different habitats such as: a) shrublands (Quintana-Ascencio *et al.* 1992; Callaway 1992; Callaway & Davis 1998; Weltzin & McPherson 1999; Rousset & Lepart 2000; Li & Ma 2003), b) pine-dominated canopies (Mosandl & Kleinert 1998; Camacho-Cruz *et al.* 2000; Fuchs & Krannitz 2000; Galindo-Jaimes *et al.* 2002), c) forest gaps (Rebertus & Burns 1997; Ke & Werger 1999; Collins & Battaglia 2002; Li & Ma 2003; Riley & Jones 2003) and d) disturbed forest (Thadani & Ashton 1995; Adams & Rieske 2000). The favourable conditions of these habitats for oak seedling establishment have been related to light availability, semi-open canopies offering a well-illuminated microenvironment that enhances seedling survival and growth but also protects the seedling from desiccation or frost damage (Callaway & Davis 1998; Gardiner & Hodges 1998).

Although it has been documented that forest edges are characterised by intermediate light availabilities (Jose *et al.* 1996; Williams-Linera *et al.* 1998; Newmak 2001), few studies have documented the presence of higher oak regeneration along forest edges with respect to adjacent forest interiors (Kramer *et al.* 1952; Wales 1972; Ranney *et al.* 1981; Crow 1988). No previous research, to my knowledge, has experimentally tested the seedling performance of different oak species in forest edges compared with the forest interior and adjacent open areas.

Edges between mature forest and open areas may present higher light availabilities, wind speed, and soil temperature, as well as lower relative humidity compared to the adjacent forest interior (see review in Chapter 2). However these edge-related responses could be ameliorated or exacerbated as a result of the type of vegetation adjoining forest fragments (Didham & Lawton 1999). The effect of different edge types in mediating forest regeneration processes is relatively unknown (Cadenasso & Pickett 2001; Laurence *et al.* 2001). The height and structure of vegetation that surrounds forest patches could influence both the overall magnitude and the maximum penetration distance of edge effects relating to microclimatic variables (Mesquita *et al.* 1999). Although most studies of forest fragments have found changes in the density and composition of tree seedlings in the edges compared with the forest interior (see review in Chapter 2), the response of oak tree seedlings to these complex environmental gradients is largely untested (but see Meiners *et al.* 2002).

Tropical Montane Cloud Forests have recently received considerable attention as they are considered to be one of the world's main centres of montane biodiversity (Webster 1995; Aldrich *et al.* 1997). Montane forests in Chiapas, as in many other mountainous regions of Latin America, have become increasingly fragmented owing to the processes of deforestation (Ochoa-Gaona & González-Espinosa 2000) and forest degradation (Ramírez-Marcial *et al.* 2000). The traditional land use patterns in the Highlands of Chiapas have supported indigenous Mayan communities for centuries, however it currently faces severe changes associated with increasing land scarcity, reducing soil fertility and increasing population density (De Jong *et al.* 1999; Ochoa-Gaona & González-Espinosa 2000; Ochoa-Gaona 2001).

In traditional shifting cultivation, forest clearings (0.5 to 2 ha) are created and the "Milpa" (corn-bean field) is cultivated for one to three years, after which it is abandoned for three to ten years favouring the growth of shrub and tree fallow. The fallow is usually cultivated again or maintained as grasslands for livestock, although occasionally a few clearings are allowed to develop into secondary forests. Such secondary vegetation fragments are in a dynamic process of change and their

regeneration will depend, among other factors, on their spatial position with respect to the forest matrix. Forest areas may therefore be bordered by different modified habitats, producing different edge types (see Chapters 2 and 3). Forests bordered by open grasslands result in an abrupt boundary that may have a higher incidence of lateral light and this may enhance development of a dense herbaceous stratum and increased seedling abundance along the edge (Lopez de Casanave *et al.* 1995). However, these edges may be more exposed to temperature and humidity fluctuations than the forest interior. The forest interior in these sites may also be relatively susceptible to changes in the microclimatic gradients (Gascon *et al.* 2000). On the other hand, forests bordered by abandoned pastures or fallows present successional vegetation that may intercept lateral light near the edge resulting in shaded edges. These edges would potentially present less herbaceous and seedling cover, but this edge type may act as a buffer that protects the forest interior from high microclimatic fluctuations (Gascon *et al.* 2000). Understanding the role of different edge types in determining tree establishment is critical to predicting forest regeneration (Mesquita *et al.* 1999) and the forest dynamics in landscapes subjected to intensive human use, such as those of Chiapas.

In the Highlands of Chiapas, oak species occur as the main component of the canopy or in association with pines. Oaks play an important role in forest regeneration because some oak species may become established in early successional stages such as abandoned crops and shrublands (González-Espinosa *et al.* 1991). The partially shaded characteristics of fallows or early successional forests in the region seems to be favourable for the germination and early establishment of oaks, as reported for *Q. crispipilis* (Quintana-Ascencio *et al.* 1992), *Q. laurina* (Camacho-Cruz *et al.* 2000), *Q. crassifolia* and *Q. rugosa* (Ramírez-Marcial *et al.* 1996). Although the secondary forest succession from abandoned crops has been previously described in the study area, the effect of anthropogenic habitat edges on tree seedling performance has never been assessed.

The purpose of this study was to examine the survival and growth of five oak species and improve the understanding of seedling performance across their potential

dispersal range. In general, I predict that seedling survival and growth will be higher at the forest edge and under microhabitats with shrub cover, as these microhabitats may have intermediate conditions of light and humidity. Species-specific hypotheses are that relatively shade intolerant species that prefer relatively xeric sites (*Q. rugosa* and *Q. segoviensis*) would demonstrate higher performance (higher survival and growth) in the grasslands. Conversely, I predict that more shade-tolerant species that prefer humid sites (*Q. laurina, Q. candicans* and *Q, crassifolia*) would have a higher performance in the edge or the forested portion of the gradient.

The second objective was to compare the interactions between edge type and distance from the edge. I hypothesised that (a) as environmental variables such as light and humidity change abruptly across hard edges, then it is expected that seedling survival and growth will similarly change markedly either side of the edge; however, this effect will be less pronounced across soft edges and (b) as changes in vegetation cover may affect the composition and abundance of tree seedling herbivores and predators (Cadenasso & Pickett 2000; Wada *et al.* 2000; Molnar *et al.* 2001; Wahungu *et al.* 2002), then it is expected that seedling predation will vary significantly across forest interior-edge-grassland gradients.

METHODS

Experimental plots

A detailed description of the study area and the experimental plots is available in Chapters 2 and 3.

Species description

Quercus species used in this study are evergreen trees and occur in the Highlands of Chiapas. These species are widely distributed both locally and countrywide (except *Q. segoviensis*, a semi-evergreen tree distributed in Chiapas and Central America). *Quercus candicans* Née*, Q. crassifolia* Humb.& Bonpl. and *Q. laurina* Humb.&

Bonpl. belong to red oaks (*Erithrobalanus* subgenus) and are more common in humid sites or more mesic habitats. *Q. rugosa* Née and *Q. segoviensis* Liebm. belong to the white oaks (*Leucobalanus* subgenus) and are more common on drier hillsides or xeric sites (González-Espinosa *et al.* 1991; González-Espinosa *et al.* 1997; Ramírez-Marcial *et al.* 1998; Alvarez-Moctezuma *et al.* 1999; Galindo-Jaimes *et al.* 2002). Acorns of these white oaks mature and drop to the ground from September to February. Germination usually occurs immediately afterwards in the case of *Q. crassifolia, Q. segoviensis* and *Q. rugosa*, while in the case of *Q. candicans* and *Q. laurina,* acorns remain dormant until the occurrence of winter rains in January-February (Chapter 5).

Acorns

From September 2000 to November 2000 acorns of the studied species (Table 6.1) were collected in Rancho Merced Bazom (*Q. laurin*a and *Q. crassifolia*), Moxviquil (Q. *segoviensis*), Mitziton (*Q. rugosa*) and Huitepec (*Q. candicans*). After collection, an equal number of acorns from each parent source were mixed together for each species. Acorn viability was tested by floating them in water, which is a reliable method to identify damaged acorns (Gribko & Jones 1995); only those, which sank, were subsequently planted. One hundred acorns were used for the measurement of acorn mass and diameter (Table 6.1). Before sowing, acorns were soaked in water for 24 hours to enhance acorn hydration. Acorns of different species were put into rectangular polystyrene containers (47 x 30 cm) filled with mineral soil (10 cm deep layer) and covered with approximate by 3 cm of pine and oak litter to increase the germination rate (López-Barrera & González-Espinosa 2001). Shoot emergence began in November for *Q. crassifolia* and *Q. segoviensis* and late December for *Q. rugosa. Q. laurina* and *Q. candicans* shoots appeared in late January. After seedling emergence, oak seedlings were individually transplanted into black plastic bags containing mineral soil (1966 cm^3). All mineral soil and leaf litter used in the nursery was collected in the forest in Rancho Merced Bazom.

Table 6.1 Main characteristics of the seedlings used in this study. Germination data were obtained in the laboratory (see details in Chapter 5, for *Q. segoviensis* germination see Chapter 4). Acorn characteristics were obtained from measurements of 100 fresh acorns. Values are means (± 1 SE). Abundance data were obtained from previous floristic inventories (González-Espinosa *et al.* 1997).

Species	Acorn mass (g)	Acorn diameter (cm)	Acorn germination (%)	Abundance in pine-oak forest
Q. candicans	4.51±0.09	2.01±0.02	86.0±2.8	Moderate
Q. crassifolia	1.99±0.05	1.33±0.02	74.0±2.2	High
Q. laurina	1.80±0.06	1.35±0.02	99.2±0.5	High
Q. rugosa	2.94±0.08	1.45±0.03	98.8± 0.8	High
Q. segoviensis	5.37±0.15	2.08±0.03	89.4±1.4	Moderate

The oak seedlings were grown in a greenhouse for six months before being planted in the experimental plots. The nursery was located at El Colegio de La Frontera Sur, in San Cristobal de Las Casas, Chiapas (2100 m altitude, 13-14° C mean annual temperature, 1160 mm mean annual rainfall). Plants were watered every three days. Only healthy seedlings showing no signs of disease or desiccation were used in the experiments. Seedlings within each species were selected to be as similar as possible in height, number of leaves and vigour. Plants with loss of some leaf area owing to attack by insects could not be avoided for some species (especially in the case of *Q. rugosa* and *Q. segoviensis*) and their damage was quantified at the beginning of the experiment.

Experimental design

Oak seedlings were establish on the sites at the beginning of the wet season (June 2001). Experimental factors were edge type (hard and soft), distance from the edge (-24, -12, 0, 12 and 24 m) and species (*Q. candicans, Q. crassifolia Q. laurina, Q. rugosa* and *Q. segoviensis*). For this study I defined the forest edge as the straight line coinciding with the bases of bordering mature tree stems (Jose *et al.* 1996; Oosterhoorn & Kappelle 2000). In the six sites (three sites of each edge type), transects parallel to the edge every 12 m were established. Ten seedlings per species (nine seedlings in the case of *Q. candicans*) were planted in a random order along

each transect at 0.8 m intervals in holes dug by trowels to a depth of approximately 20 cm. Transplanting was completed during one day (9 July 2001). Each of the 1470 seedlings was individually tagged using a numbered plastic tag attached to the stem by a loose wire thread at ground level.

After being transplanted, the seedlings were monitored every two months for 321 days. Seedling height, basal diameter, number of leaves, number of damaged leaves and a categorical value for insect damage were recorded for each seedling. Each seedling was scored as undamaged, damaged by herbivores, mechanically damaged or dead from other causes. Each herbivore damages seedlings in a unique way, allowing scoring damage by specific herbivore. Small mammals clip seedling stems at the base, approximately 2-4 cm above the soil surface. Invertebrate damage consists mostly of defoliation or root damage. Percentage of defoliation was assessed by a categorical estimation (0: no defoliation, 1: low, 2: medium and 3: high defoliation). Leaf area loss was estimated visually as a fraction of extrapolated extent of leaf area. Every two months (coinciding with the seedlings evaluation) microenvironmental variables were measured. Soil moisture (% expressed on a fresh weight basis) was estimated on two cylindrical samples (18 cm^3) randomly taken in each transect at a depth of 4 cm within mineral soil.

Photosynthetically active radiation (PAR μmol m^{-2} s^{-1}) was measured using a ceptometer (Sunfleck Decagon Pullman, Washington, USA). Four measurements (average of 30 readings) were taken every five metres along each transect (distance from the edge) at the top of the plants, which were then averaged to provide one value per transect.

Herbaceous cover and composition

Before planting the seedlings, the ground vegetation cover and the shrub stratum were characterised. The line-intercept method for assessing cover was used (Mueller-Dombois & Ellenberg 1974). A metre tape was laid out (15-20 cm above the ground) and the crowns that overlapped or intercepted the line were recorded by

species. The accumulated length occupied by any one species out of the total metre tape length used for the sample was used to calculate the percentage cover for that species. The metre tape was also used to measure two understorey vegetation layers separately. The strata were 1) the prostrate herbaceous layer (<15 cm) and 2) tall herbs or shrubs (>15 and <50 cm); the height of this last layer was also measured for each species.

Statistical analysis

Relative growth rates (RGR) were calculated using basal area (sum of the basal area of all the stems present for each seedling) and stem height (considering only the tallest stem present for each seedling). RGR was calculated using the formula: $R=(\ln V_2-\ln V_1)/(T_2-T_1)$, where R is the rate of increment, V_1 and V_2 are any growth variable at time 1 and time 2. T_2 and T_1 are the period of time (Hunt 1990).

The influence of edge type (hard and soft), distance from the edge (-24, -12, 0, 12 and 24 m) and species (*Q. candicans, Q. crassifolia, Q. laurina, Q. rugosa* and *Q. segoviensis*) including all their possible interactions were tested with an ANOVA. Dependent variables were proportion of seedling survival (transformed with arcsine square root), number of leaves ($\log_{10}$ transformed and using the initial number of leaves as a covariate), difference in the proportion of seedlings with any level of defoliation, RGR of basal area, RGR of stem height and difference in stem height/diameter ratio. Growth variables for each species at the end of the experiment as a function of the experimental factors are presented in the Appendix 5 (Table A.5.1). For data analysis, the measurement unit used was the average of ten seedlings (nine seedlings in the case of *Q. candicans*) within each distance from the edge (at the beginning and at the end of the experiment). Seedlings considered as dead at the end of the experiment were excluded from any of the growth analyses.

The variation in the degree of defoliation had two components: the proportion of leaves damaged and a categorical value (1 to 3) of lost leaf area. A relative index of leaf damage was calculated, by first transforming the proportion of leaves damaged

into a categorical variable with four levels (1 to 4), then adding both categorical values together to provide an overall index. The difference between the initial and final status of the seedlings was analysed using ANOVA (SPSS v.10.0.1) for all the experimental factors and their interactions.

The number of seedlings that produced more than one stem during the study period was analysed with a Chi-Square distribution test for the association between edge type and distance from the edge and a separate analysis for the species factor (Crosstabs procedure, SPSS v. 10.0.1). The shape of the curves of cumulative proportion of surviving seedlings over time was compared with a survival function using the Wilcoxon-Gehan statistic and pairwise comparisons (Life table procedure, SPSS v.10.0.1). The tested factors were edge type, distance from the edge and species.

Soil moisture (arcsine transformed), PAR reaching the soil surface ($\log_{10}$ transformed), total vegetation cover (arcsine transformed) and mean height of the prostrate vegetation layer ($\log_{10}$ transformed) in each transect were analysed using ANOVA testing the effect of date of sampling (only for soil moisture and PAR), edge type and distance from the edge. Tukey's HSD multiple comparisons were used to detect significant differences among treatment means (using SPSS v.10.0.1).

Herbaceous and shrub species diversity were calculated in each transect (distance from the edge) in each study site using Shannon-Wiener's diversity index ($H = -\Sigma (p_i)(\ln p_i)$) and Evenness index ($J = H / \ln (S)$), where S is the total number of species in the habitat). These indices were calculated using Species Diversity and Richness (PISCES v. 2.3). Significant differences in species diversity and evenness between distances from the edge and edge types were examined using single-factor ANOVA. All full ANOVA tables are presented in Appendix 5 (Tables A.5.2-A.5.8) in the same order as they were reported in the results section. Negative distances indicate metres from the edge (distance 0) into the grasslands. In the text, means are given ± 1 SE unless otherwise stated.

RESULTS

Seedling survival

After 321 days (from July 2001 to May 2002), from the 1470 seedlings established initially, 14.3% were recorded as dead. The definition of death was complicated by the fact that oak seedlings tend to resprout following stem death. At the end of the experiment, seedlings previously scored as dead but later resprouting were not considered as dead seedlings. However, a proportion of the seedlings that at the end of the experiment were scored as dead may resprout in the future.

The survivorship of seedlings was affected by the interaction between edge type and distance from the edge (Table 6.2; Fig. 6.1a). In sites with soft edges, mortality was significantly higher at the edge and within the forest (0, 12 and 24 m) than within the grasslands (-12 and -24 m). In sites with hard edges seedling survival was not affected by distance from the edge (ANOVA, $P>0.05$). Mortality within the forest was mostly due to attack by rot (25.3 ± 5.3% of the total dead seedlings), apparently caused by a pathogen or fungal attack (18.4 ± 4.9%), root damage by herbivores (6.7 ± 3.1%) or rodent damage (2.2 ±1.4%); for 47.3 ± 3.2% of the seedlings, the cause of mortality was not determined. In hard edges an opposite trend was recorded; higher mortality was observed at 24 m into the grasslands compared to the edge and the forest interior. Mortality across the grasslands of sites with hard edges was mostly due to shoot desiccation (38.6 ± 8.6%) or root damage by herbivores (13.4 ± 5.6%); for 45.0 ± 8.8% of the seedlings the cause of mortality was not determined. Stems clipped by mice were more common in the grasslands of soft edges than in hard edges (16.0% vs. 7.1%). No evidence was found for frost heaving causing seedling mortality in open areas.

Survival probabilities changed between species but only within the forest, where there was a decrease in seedling survival in the case of *Q. crassifolia* within the forest compared with seedlings planted in the grasslands (Fig. 6.1b). This was mostly due to rot (44% of the seedlings), the rest of the dead seedlings in the forest stands

Table 6.2 ANOVA of the influence of experimental factors: T: Edge Type (hard and soft), D: Distance from the edge (-24, -12, 0, 12 and 24 m), S: Species (*Q. candicans, Q. crassifolia, Q. laurina, Q. rugosa* and *Q. segoviensis*) and their interactions on total seedling survival (TSS), leaf number (LN), difference in stem height/diameter ratio (H/D), RGR of basal area (RGRBA), RGR of maximum stem height (RGRSH) and the difference in the proportion of defoliated seedlings (DS). The covariate in the case of the number of leaves was the initial number of leaves of the seedlings. * = ($P \leq 0.05$), ** = ($P \leq 0.01$), *** = ($P \leq 0.001$), ns = ($P > 0.05$).

		TSS		LN		H/D		RGRBA		RGRSH		DS	
Source of variation	*df*	S.S	*F*	S.S	*F*	S.S	*F*	S.S	*F*	S.S	*F*	S.S	*F*
T	1	0.558	8.96**	0.058	2.56ns	2131.1	16.89***	0.010	7.72**	0.0029	32.09***	0.564	7.51**
D	4	0.831	3.33*	4.4495	49.02***	3334.5	6.61***	0.120	22.78***	0.0015	4.26**	1.099	3.65**
S	4	2.350	9.43***	3.311	36.11***	2940.5	5.83***	0.027	5.26***	0.0070	19.80***	2.335	7.76***
T X D	4	1.602	6.43***	0.276	3.00*	308.59	0.61 ns	0.012	2.33ns	0.0015	4.33**	1.122	3.73**
T X S	4	0.165	0.66ns	0.125	1.36ns	61.39	0.12ns	0.004	0.75ns	0.0000	0.02ns	0.178	0.59ns
D X S	16	2.328	2.33**	0.861	2.35**	2400.3	1.19ns	0.019	0.91ns	0.0016	1.17ns	1.853	1.54ns
T X D X S	16	0.701	0.70ns	0.103	0.28ns	1283.3	0.64ns	0.011	0.51ns	0.0018	1.26ns	1.041	0.86ns
Covariate	1			0.379	16.55***								
Error	100	6.231		2.271		12615.4		0.131		0.0089			7.514

wilted without any apparent mechanical or pathogenic damage. The pattern of seedling survival over time differed among species (Wilcoxon-Gehan χ^2 =92.46; df =4; P<0.001) and between distances from the edge (χ^2 =52.59; df =4; P<0.001; Fig. 6.2) but not between edge types (P>0.05).

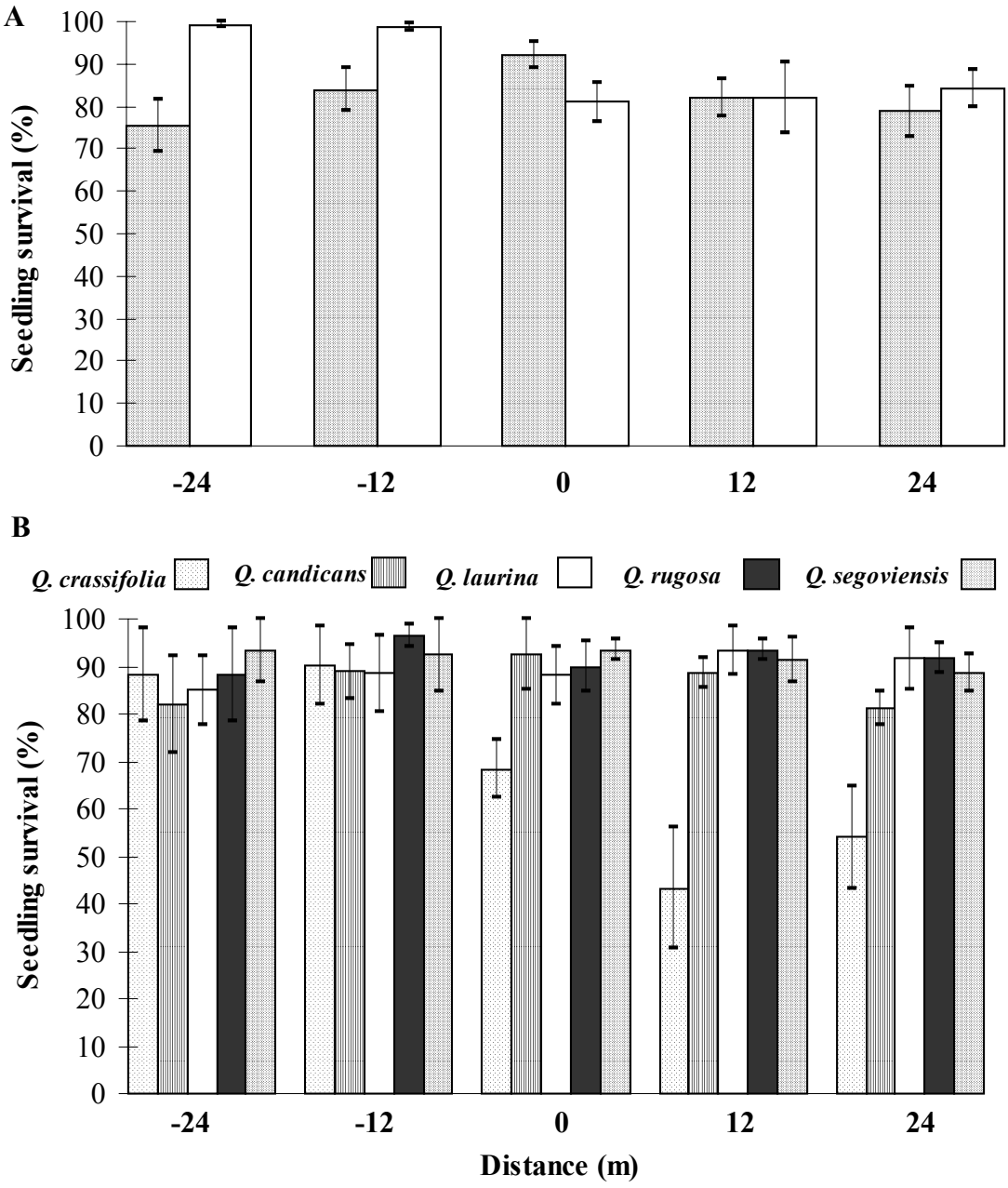

Fig. 6.1 Seedling survival (mean ± 1 SE %) after 321 days as a function of A) distance from the edge (negative distances indicate metres from the edge into the grassland) and edge type: hard (shaded bars) and soft (open bars) and B) species at different distances from the edge.

The probability of seedling survival decreased with time more rapidly at the edge and 12 m into the forest than at other distances. The survival probability of *Q. crassifolia* seedlings started to decrease in November 2001 and continued to decrease gradually until May 2002 when there was a high mortality of this species (Fig. 6.2).

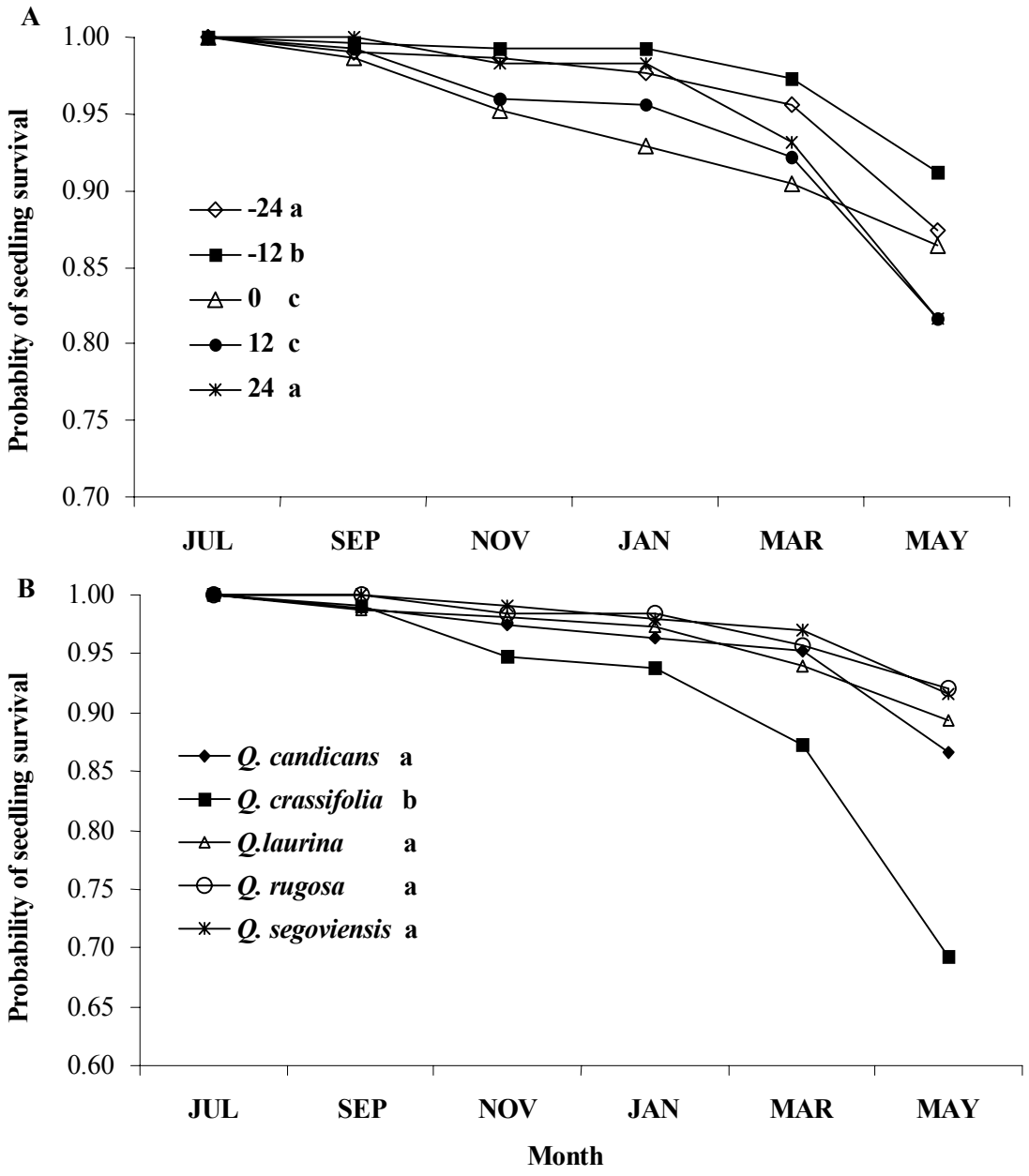

Fig. 6.2 Probability of seedling survival from July 2000 to May 2001 as a function of A) distance from the edge (negative distances indicate metres from the edge into the grassland) and B) species. Different letters after the graph legends indicate significant differences in the overall shape of the curves as determined by the Wilcoxon-Gehan comparisons (P<0.05).

Effects of edge type and distance from the edge on seedling growth

At the end of the study period the relative height growth rate of surviving seedlings changed significantly in relation to distance from the edge but only in the case of soft edges (Table 6.2). Seedlings planted at 12 m from the edge into the grassland in soft edges had higher increments in maximum stem height than seedlings planted at the edge (Fig. 6.3a). This seedling response coincides with the highest cover of shrubs and tree saplings and the tallest herbaceous stratum recorded within the grasslands (Table 6.3).

Relative growth rates calculated using basal area were significantly affected by the main experimental factors: edge type and distance from the edge (Table 6.2). Seedlings had a higher increment in basal area in hard (0.063 ± 0.006 mm^2 mm^{-2} $month^{-1}$) than in soft edges (0.047 ± 0.005). Seedlings planted in the grasslands (-24 and -12 m) accumulated higher basal area (0.082 ± 0.008 and 0.093 ± 0.008, respectively) than seedlings growing in the edge (0.047 ± 0.008) or in the forest interior (12 and 24 m; 0.027 ± 0.006 and 0.024 ± 0.006, respectively). The interaction between edge type and distance from the edge was marginally not significant (P= 0.061).

At the end of the study period the number of seedlings that produced new stems varied in relation to the edge type and distance from the edge (χ^2 =7.99; df =3; P=0.046). Seedlings planted in the grasslands (-24 and -12 m) of hard edges produced more stems (17 and 16 multi-stemmed seedlings, respectively) compared to the edge (two multi-stemmed seedlings). In the soft edges, 14 seedlings planted 24 m into the grassland produced more than one stem, however only 4 seedlings were recorded with more than one stem 12 m into the grassland. In all the study sites, within the forest interior, seedlings generally did not produce more stems (only two cases recorded within the forest) but in fact significantly reduced the number of stems that they possessed at the beginning of the experiment (χ^2 =20.79; df =4; P<0.001). Sixty-nine seedlings (from this 53 were *Q. crassifolia* seedlings) lost stems within the forest compared to only 14 seedlings planted in the grasslands.

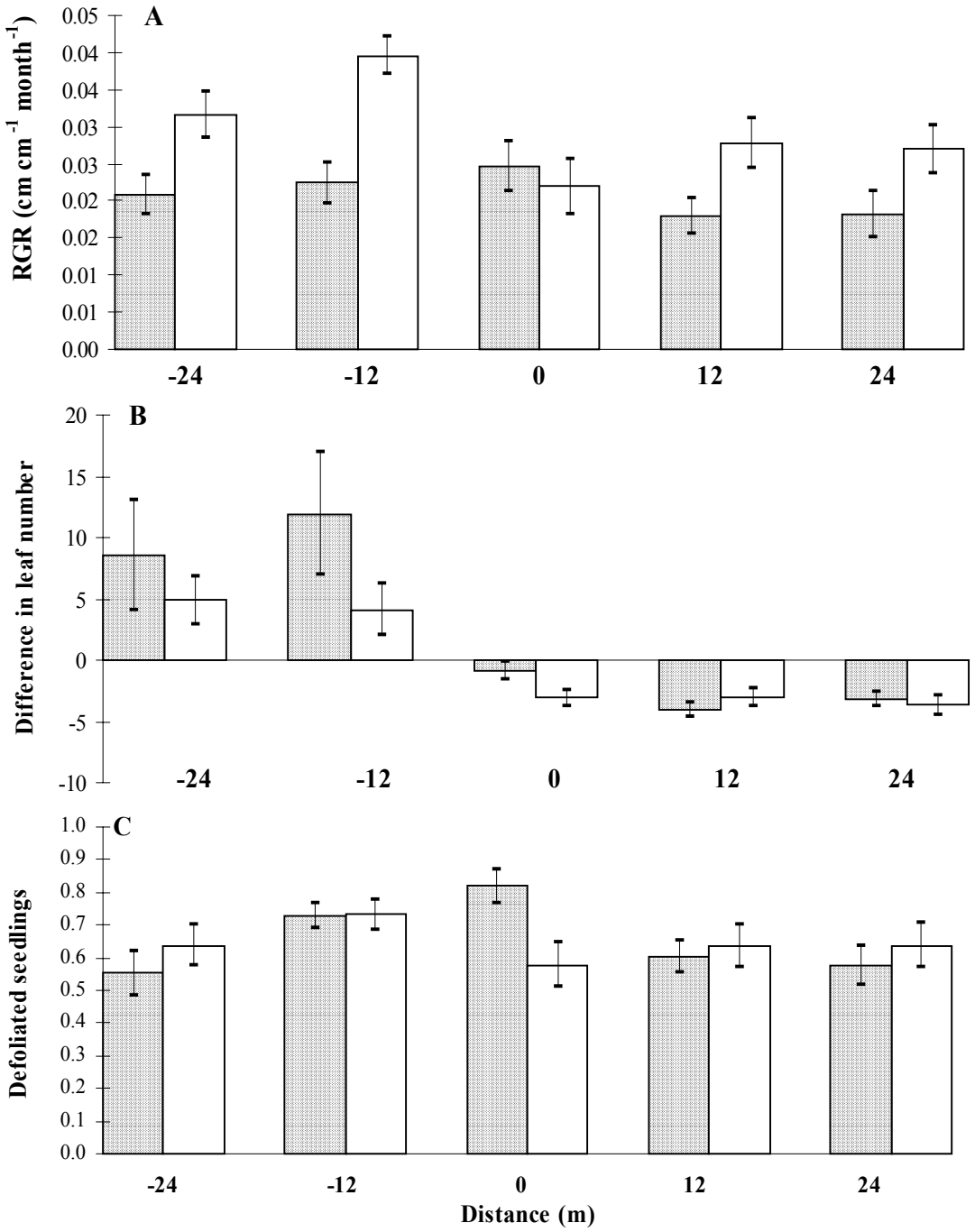

Fig. 6.3 Effect of edge types (hard: shaded bars and soft: open bars) and distance from the edge (negative distances indicate metres from the edge into the grassland) on A) RGR of stem height, B) difference in leaf number during the study period, and C) proportion of seedlings showing any level of defoliation at the end of the experiment. Values are means ± 1 SE.

The difference in the number of leaves was affected by the interaction between edge type and distance from the edge (Table 6.2). From July 2001 to May 2002 there were

increases in mean leaf number in seedlings planted in grasslands and decreases in seedlings planted within the forest, but this pattern was more pronounced in sites with hard edges (Fig. 6.3b).

Herbivore damage on seedlings was significantly affected by the interaction between edge type and distance from the edge (Table 6.2). In Fig. 6.3c the final proportion of seedlings defoliated is presented. This variable had the same trend as the difference between the initial and final condition. More seedlings presented defoliation at the edge and 12 m into the grassland of hard edges compared with the other experimental distances. In the case of soft edges, there were no significant differences along the grassland-edge-forest gradient (ANOVA, $P>0.05$).

The difference in the levels of seedling defoliation as determined by the leaf damage index during the study period was affected by the distance from the edge ($F=8.76$; df=4; 100; $P<0.001$). Experimental seedlings planted in the edge and in the forest were significantly more defoliated than seedlings planted in the grassland. Seedlings growing in the grasslands displayed reduced levels of damage (i.e. by possessing lower damage in new leaves or by the abscission of damaged leaves) compared to their initial condition, whereas the opposite pattern occurred within the forest (Fig. 6.4).

Significant differences were detected among edge types and distances from the edge (Table 6.2) on the difference between the initial height/diameter ratio at the end of the experiment. Seedlings growing in soft edges (2.3 ± 1.4) and within the forest interior (Fig. 6.5) allocated more resources to increase stem height over diameter, whereas in hard edges (5.3 ± 1.5) and in the grasslands habitats (Fig. 6.5) seedlings presented lower stem height/diameter ratios. Seedlings growing along the edge, regardless the edge type presented lower difference in their height/diameter relative to their original condition (Fig. 6.5). A regression analysis was made to determine changes in stem height/diameter ratio at the end of the experiment along a gradient of light intensity. The stem height/diameter ratio decreased as the light (PAR) increased (Fig. 6.5).

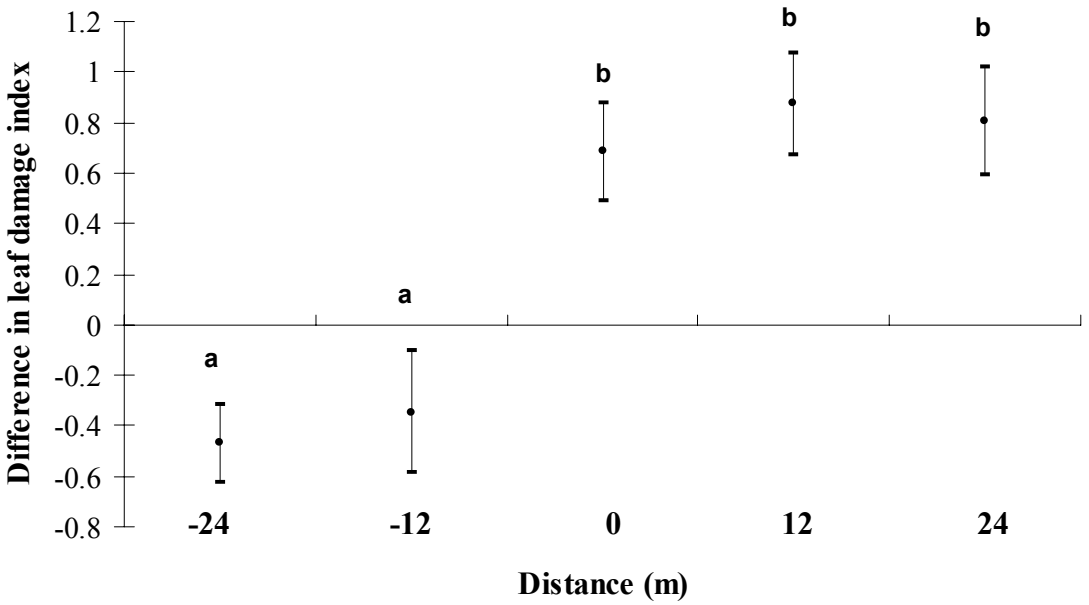

Fig. 6.4 Difference in the leaf damage index at the end of the experiment as a function of distance from the edge (negative distances indicate metres from the edge into the grassland). Values are means ± 1 SE. Different letters indicate significant differences as determined by Tukey HSD comparisons (P<0.05).

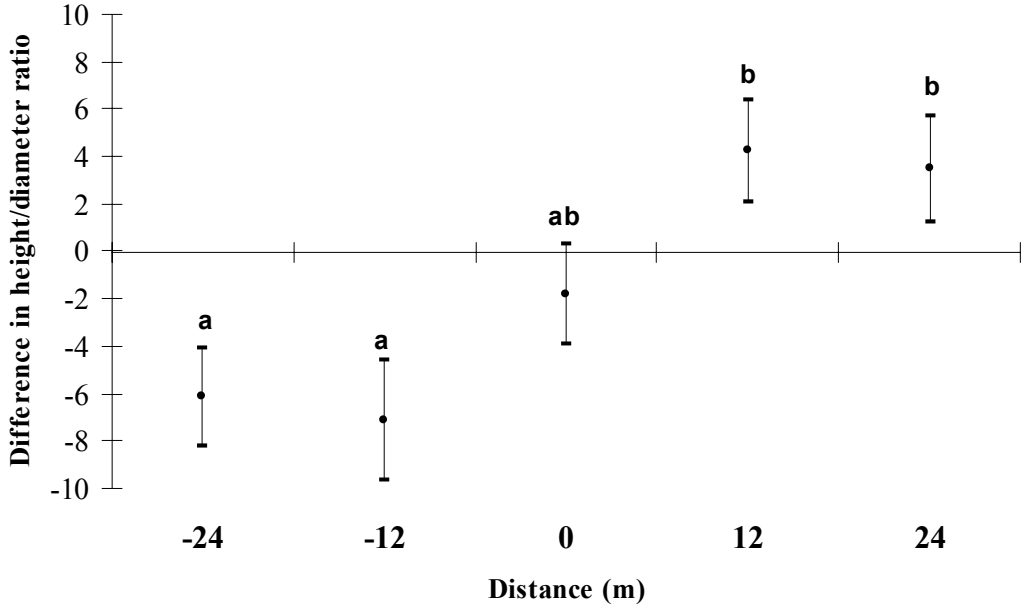

Fig. 6.5 Difference in the seedling height/diameter ratio at the end of the experiment as a function of distance from the edge (negative distances indicate metres from the edge into the grassland). Values are means ± 1 SE. Different letters indicate significant differences as determined by Tukey HSD comparisons (P<0.05).

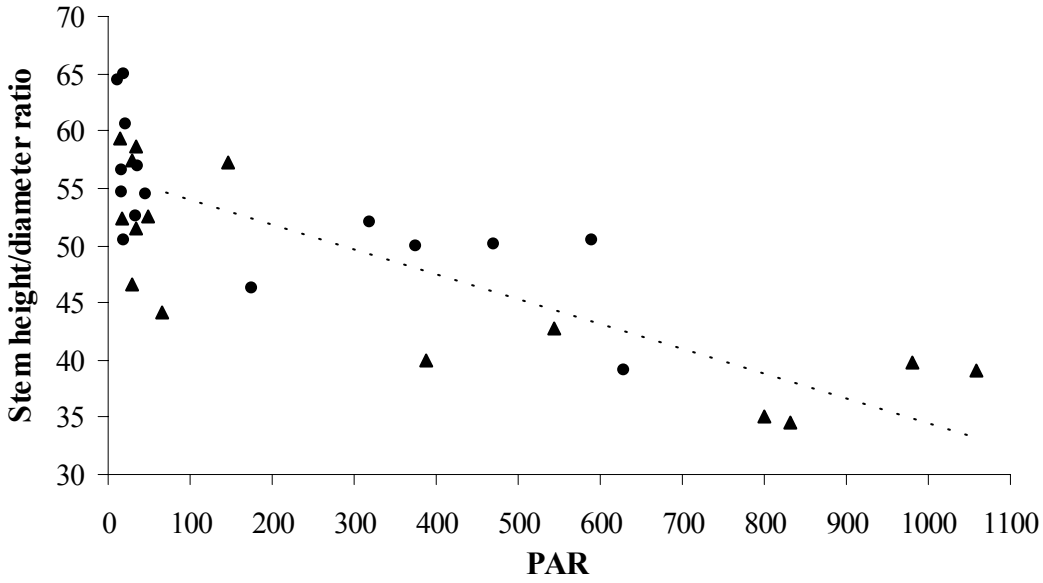

Fig. 6.6 Relationship (y = 55.6 - 0.02 * x, R^2= 0.62) between the mean seedling height/diameter ratio at the end of the experiment and the mean photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}). Symbols as circles represent means from sites with soft edges and triangles sites with hard edges.

Differences between species in seedling growth

Quercus species showed different RGR of stem height (Table 6.2); *Q. rugosa* presented higher increments in stem height (0.0386 ± 0.0019 cm cm^{-1} $month^{-1}$) than *Q. candicans* (0.0234 ± 0.0021), *Q. crassifolia* (0.0192 ± 0.0019), *Q. laurina* (0.0218 ± 0.0023) or *Q. segoviensis* (0.0230 ± 0.0019). Relative growth rates calculated using basal area were significantly affected by the factor 'species' (Table 6.2). The RGR of basal area was significantly higher for *Q. rugosa* (0.071 ± 0.009 mm^2 mm^{-2} $month^{-1}$) and *Q. laurina* (0.069 ± 0.007) compared to *Q. segoviensis* (0.036 ± 0.008). In the case of *Q. candicans* (0.054± 0.007) and *Q. crassifolia* (0.044 ± 0.010), intermediate values were recorded.

There were significant differences between species in the difference in stem height/diameter ratio (Table 6.2). At the beginning of the experiment *Q. candicans* (54.1 ± 1.6) and *Q. segoviensis* (53.3 ± 1.7) seedlings allocated greater biomass to height growth over diameter than *Q. crassifolia* (47.4 ± 1.1) and *Q. rugosa* (45.23 ±

1.3). This pattern was similar at the end of the experiment, except in the case of *Q. laurina* that at the beginning of the experiment presented the highest stem/diameter ratio relative to the other species (59.3 ± 1.4) and by the end of the experiment decreased the ratio to an intermediate value relative to other species (50.8 ± 1.6).

The variation in defoliation levels (leaf damage index) between the start and the end of the experiment was significantly different between species (F=6.65; df=4,100; P<0.001). In *Q. segoviensis* seedlings, the degree of leaf damage increased significantly during the experiment and together with *Q. crassifolia,* these species presented a relatively high degree of defoliation. The species with least increase of defoliation throughout the experiment was *Q. laurina. Q. candicans* and *Q. rugosa* seedlings decreased their degree of defoliation throughout the experiment (Fig. 6.7). Leaf damage appeared to be caused mostly by lepidopteran larvae as indicated by the characteristics of the damage, since these larvae usually remove pieces from the leaf surface. In a few cases damage by other predators was recorded, such as slugs (*Gasteropoda*), which tend to leave more of the leaf vascular system intact so that after feeding only the leaf skeleton remains.

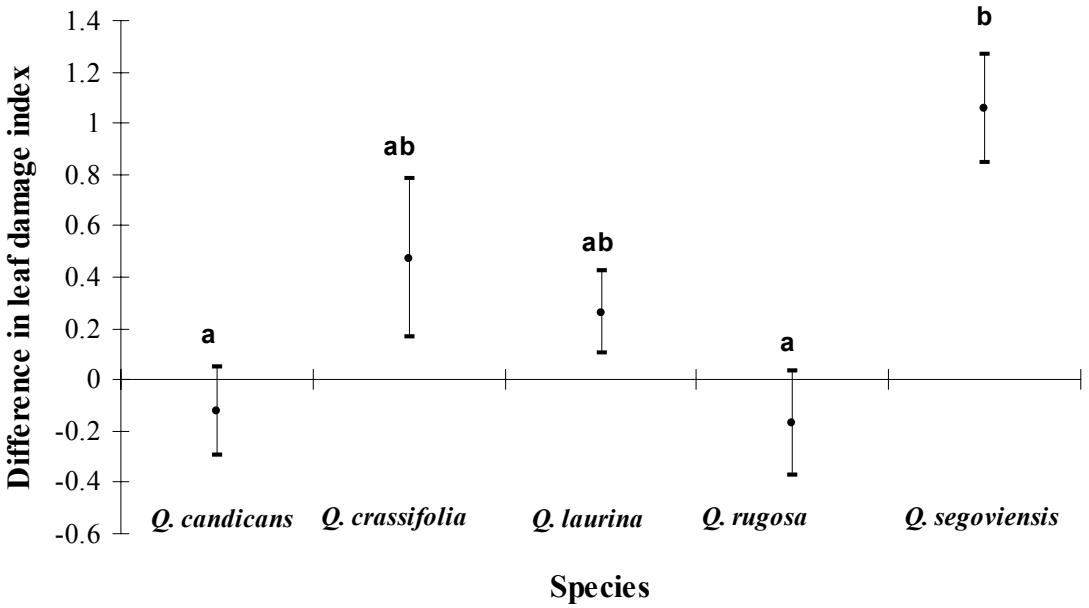

Fig. 6.7 Difference in leaf damage index at the end of the experiment as a function of species (negative distances indicate metres from the edge into the grassland). Values are means ± 1 SE. Different letters indicate significant differences as determined by Tukey HSD comparisons (P<0.05).

Significant differences in the proportion of defoliated seedlings between species were recorded (Table 6.2). *Q. laurina* and *Q. rugosa* (0.81 ± 0.03 and 0.80 ± 0.02, respectively) had a higher proportion of defoliated seedlings at the end of the experiment compared with *Q. candicans* (0.65 ± 0.04), *Q. crassifolia* (0.47 ± 0.04) and *Q. segoviensis* (0.52 ± 0.03).

There were also significant differences between the species (χ^2 =12.71; df =3; *P*=0.005) in new stem production; *Q. crassifolia* had more seedlings that produced more than one stem (24 seedlings) than the other species, followed by *Q. laurina* (15), *Q. segoviensis* (9) and *Q, rugosa* (7). *Q. candicans* seedlings never produced more than one stem.

The differences in leaf number between species varied along the distances from the edge (Table 6.2). *Q. laurina* seedlings growing in the grasslands (-24 and -12 m) had a higher increment in leaf number compared to the rest of the species (Fig. 6.8).

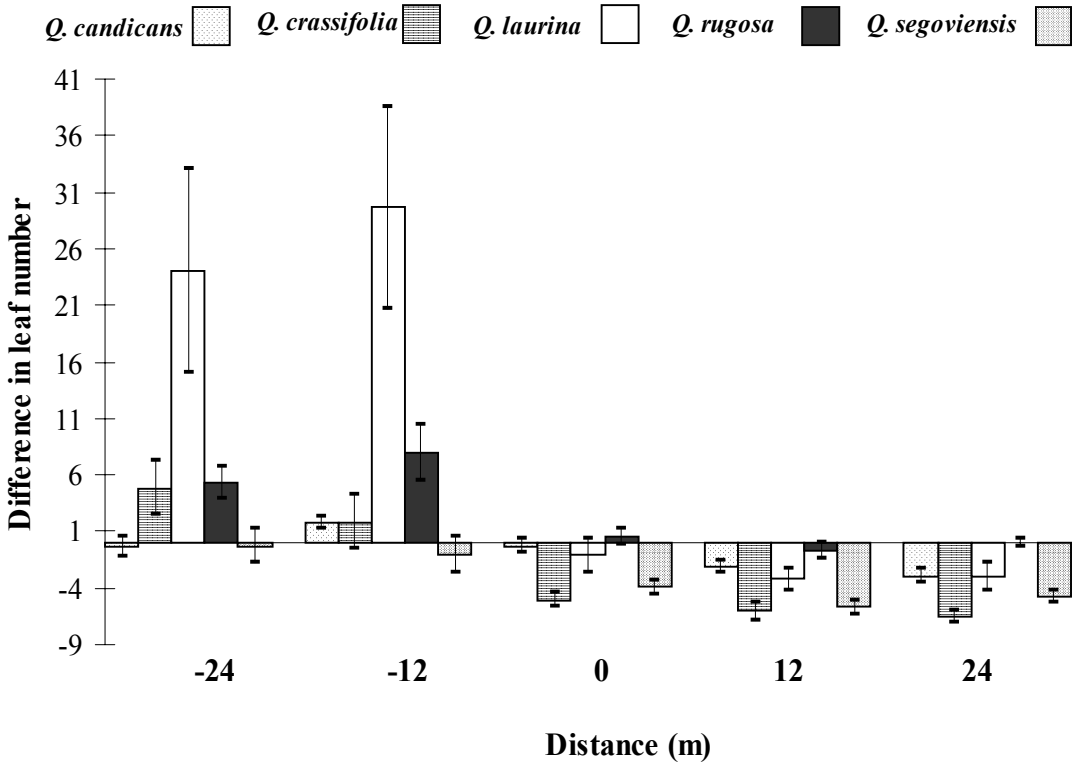

Fig. 6.8 Effect of species and distances from the edge (negative distances indicate metres from the edge into the grassland) on the differences in leaf number during the study period. Values are means ± 1 SE.

Environmental variables

There were no significant differences in soil moisture among edge types and distances from the edge (P>0.05; Table 6.3). Soil moisture varied with the sampling dates (F=265.96; df=5, 120; P<0.001; Fig. 6.8).

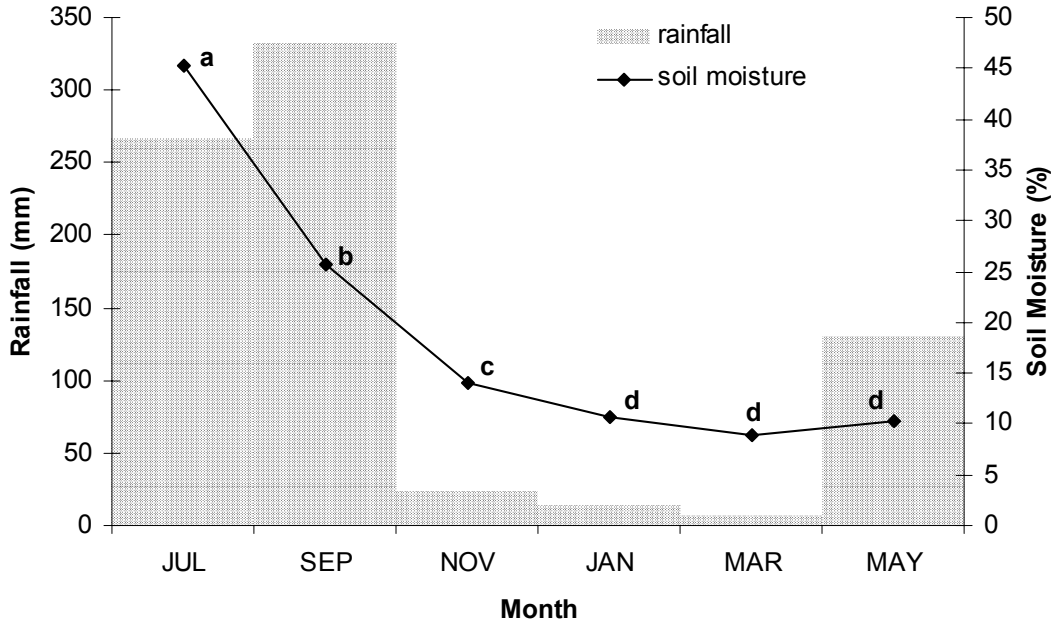

Fig. 6.8 Total rainfall (mm) and mean soil moisture (% of fresh mass) from 2000 to 2001 in the study area. Rainfall data were obtained from the National Water Commission and recorded at the meteorological station "Chilil" (latitude N 16^{o} 40'30'', longitude W 92^{o} 29'10'' and altitude 2200 m), Huixtan municipality, Chiapas, Mexico. Different letters for soil moisture indicate significant differences as determined by Tukey HSD comparisons (P<0.05).

PAR reaching the top of the plants was affected by the interaction between edge type and distance from the edge (F=2.46; df=4, 120; P=0.049). The change in light condition was more abrupt crossing the edges of hard edges than soft edges (Table 6.3). Total vegetation ground cover was not affected by the interaction between edge type and distance from the edge, and was only affected by distance from the edge (F=25.17; df=4, 20; P<0.001). Total species diversity was similar along distances from the edge and edge types (ANOVA, P>0.05). Species evenness was affected by distance from the edge (F=2.99; df=4, 20; P=0.043), however none of the pairwise comparisons were significant (Tukey HSD, P>0.05). The maximum height of

Table 6.3 Means (± 1 SE) of vegetation (percentage relative to 100 % cover) and environmental variables on transects from the edge (0 m) into the grassland (negative distances) and into the forest (positive distances). Table values are means for each edge type; hard edges (sites PP, NP and MP) and soft edges (sites PM, MD and NM). Environmental variables are means of five temporal replicates during the experiment.

	HARD					SOFT				
	-24 m	**- 12 m**	**0 m**	**12 m**	**24 m**	**-24 m**	**- 12 m**	**0 m**	**12 m**	**24 m**
Dead wood (%)	0	0	0	0	3.3±3.3	2.9±2.9	4.0±3.2	3.0±1.6	0.7±0.7	0.8±0.8
Leaf litter (%)	0.4±0.3	0.2±0.1	73.2±9.8	77.5±5.2	71.1±8.4	0	3.7±0.7	45.5±16.2	62.5±9.0	62.2±16.0
Gramineous species (%)	39.1±17.0	36.6±15.3	1.5±1.5	0.9±0.9	0	29.5±14.0	3.6±2.2	13.2±10.1	0	0.3±0.3
Herbs (%)	60.4±17.0	62.2±14.9	13.3±6.8	5.1±1.5	4.8±2.6	65.5±12.2	57.4±20.9	18.0±10.2	5.1±2.7	9.5±5.3
Ferns and epiphytes (%)	0	0.5±0.5	3.1±1.2	6.1±1.5	8.2±1.9	0	6.3±6.3	10.9±4.1	17.4±2.9	10.0±8.1
Vines (%)	0	0	0.2±0.2	2.4±1.5	3.0±0.9	0	1.0±0.6	0.6±0.4	2.6±1.9	2.2±2.2
Shrubs and tree saplings (%)	0	0.5±0.5	8.8±3.7	8.0±4.2	9.5±4.0	2.1±1.2	24.0±18.1	8.7±2.6	11.8±5.1	14.8±6.1
Herbaceous height (cm)	12.4±0.4	12.0±0.3	16.5±1.1	21.1±1.4	21.3±1.7	23.4±0.9	37.9±6.7	19.0±1.1	26.5±1.3	22.8±1.6
Soil moisture (%)	18.1±2.3	20.1±2.8	19.2±2.5	19.1±2.5	19.3±2.2	18.5±2.4	19.5±2.3	19.3±2.2	19.1±2.2	18.7±2.2
PAR (μmol m^{-2} s^{-1})	614.8±125.2	533.0±135.3	73.8±28.5	21.8±7.7	31.0±2.5	383.2±47.5	233.6±78.4	19.4±2.5	17.8±1.8	31.0±11.0

herbaceous stratum (<50 cm) increased in the grasslands (-12 and –24 m) in both edge types. However, in soft edges the prostrate understorey layer was significantly higher 12 m from the edge into the grassland, compared to the rest of distances from the edge (F=4.93; df=4, 20; P=0.006; Table 6.3).

DISCUSSION

Edge type and distance effects on seedling performance

This study showed that variation in the land cover types adjacent to forest areas influenced oak seedling performance along the forest-edge-pasture gradient. These differences were associated with changes in the light conditions along this gradient resulting from changes in vegetation structure.

My initial prediction was that oak seedlings would have higher seedling survival along the edge. This was true, but only in hard edges, with respect with the adjacent forest and grassland. Hard edges presented intermediate light availabilities (mean value of 74 μmol m^{-2} s^{-1}) between the adjacent open area and the forest interior, whereas the light conditions recorded in soft edges were similar to those prevailing in the adjacent forest interior (mean of 19 μmol m^{-2} s^{-1}). Seedling performance responded to these differences. The intermediate light conditions within sites with soft edges were provided by the microsites at 12 m and 24 m into the grassland (233-383 μmol m^{-2} s^{-1}), where nearly all of the seedlings planted survived at the end of the study period. The optimal seedling performance (highest survival and stem growth rate) was recorded at 12 m from soft edges into the grasslands, which is the microsite that presented higher shrub (24%) and herb cover (57%) and the tallest herbaceous stratum (31-45 cm), as was expected. This suggests that herbaceous cover may be as beneficial for oak regeneration as a homogeneous shrub cover if herbs (such as *Salvia cinnabarina* and *Tagetes nelsonii*) form a tall stratum that provides intermediate levels of light.

Intermediate levels of light result in higher seedling growth rates compared with seedlings growing in full sunlight conditions or shaded microhabitats. Gardiner & Hodges (1998) found that *Q. pagoda* seedlings growing in shade houses at 53% and 27% of sunlight availability after two years were on average 146% taller than seedlings that received 100% or 8% sunlight and presented similar accumulation of root and shoot biomass. Optimal seedling growth under various light conditions has been reported for seedlings growing in shade houses: 56% for *Q. petraea* (Jarvis 1964b), 50% for *Q. douglassi* (Callaway 1992), 68% for *Q. ilex* (Rey-Benayas 1998) and 30% for *Q. rubra* (Phares 1971).

Results of shade-house experiments are difficult to extrapolate to field conditions due to the uniform light provided by shade cloth and because the optimal light conditions depend on the levels investigated by the experiments. However, several field studies have indicated that moderate forest disturbance and therefore partial shade appears to benefit oak regeneration. Quintana-Ascencio *et al.* (1992) found higher survivorship and growth rates of experimentally transplanted *Q. crispipilis* seedlings and saplings in shrublands and mid-successional forest than in mature forests, and Camacho-Cruz *et al.* (2000) documented, after 18 months, higher survival of *Q. laurina* seedlings in open pine-dominated stands (30-44% canopy openness) than in pine-oak forest or old-growth forest.

From the present results, mortality within the forest was apparently due to the combination of several factors, but unfortunately, the direct cause of mortality could not be determined for most seedlings. Quintana-Ascencio *et al.* (1992) recorded that *Q. crispipilis* seedling mortality was related to high canopy cover (>80%) in forested stands and was mostly due to damping off. Within the oak canopy there may be also a higher concentration of species-specific soil pathogens (Packer & Clay 2000). Low light levels under closed canopies decrease temperature and may increase soil and air humidity, creating a more favourable environment for pathogen attack on seedlings, additionally litter accumulation could enhance seedling mortality by providing a more favourable environment for fungal attacks (Grime 1966). Robin *et al.* (2001) found that root infections of oak seedlings were more severe when seedlings were

exposed to flooding compared to non flooded seedlings. They reported that fungal attack affects the plant water relations by decreasing the stomatal conductance resulting in wilting and mortality. Therefore in this study, an interaction of several factors such as shade-induced growth patterns, excessive moisture and fungal and insect attacks could have affected the seedling survival within the forest interior.

Stem height/diameter ratio

In this experiment, seedlings planted in sites with soft edges along the forest-edge-pasture gradient presented higher height/diameter ratios than seedlings planted in sites with hard edges. Height growth and diameter growth may represent important trade-off relationships: gaining height is important to compete with neighbours, but greater height growth may be attained at the cost of stem diameter growth which is necessary to support the stem mechanically and physiologically (Sumida *et al.* 1997). Thadani & Ashton (1995) found that seedlings of *Q. leucotrichophora* in a Himalayan forest presented higher height/diameter ratios of stems when seedlings were growing under a closed canopy, while the opposite pattern was recorded when seedlings were growing in moderately disturbed stands. They found that the height/diameter ratio of the seedlings increased with the canopy cover. Similar relations were reported here (using PAR), suggesting that oak seedling growth responses along the forest-edge-pasture gradients are determined mainly by the patterns of light availability along such gradients. Intermediate values of stem/diameter ratio were recorded in both edge types, suggesting that some seedling growth responses may present intermediate levels, as was hypothesised along the edges.

My second hypothesis stated that the abrupt change in the microclimatic gradients crossing hard edges would be associated with abrupt changes in most of the response variables investigated, however, contrary to my expectations, height growth rates did not vary abruptly crossing the hard edges as the incidence of light did. Height growth rates were equally low within the forest and the grasslands. A likely explanation for the reduced stem growth in the full sunlight conditions is that the

biomass allocation pattern favoured root growth. Under full sunlight conditions the relatively high vapour pressure deficit would typically lead to a high transpiration rate and eventually a greater likelihood of seedling moisture stress. By favouring root growth, seedlings increase their water absorbing capacity (Gardiner & Hodges 1998). Also, seedlings planted in grasslands in sites with hard edges produced more new leaves than the seedlings in grasslands in soft edges. Similarly, some studies have reported an increase in the number of leaves as canopy openness increases for *Q. crispipilis* (Quintana-Ascencio *et al.* 1992), *Q. michauxii* (Collins & Battaglia 2002) and *Q. leucotrichofora* (Thadani & Ashton 1995).

Ke & Werger (1999) documented that *Q. aliena* developed more but smaller leaves in light than in shade. Lower leaf area ratio in xeric sites is important to avoid potential water stress by minimising transpiring tissue (Danner & Knapp 2001; Riley & Jones 2003). Although not measured in this study, I observed that only in the case of *Q. laurina* did leaves appear to be smaller in open sites than in shaded sites, whereas for the other species no differences were noted. This may be because the other species presented a well-developed root system that compensated for the potential higher levels of evapotranspiration under full sunlight conditions.

Seedling defoliation

In this experiment, I found that seedlings growing in the forest and forest edge presented higher defoliation, apparently caused by lepidopteran larvae, compared with seedlings growing in grasslands, regardless of the edge type. Similar changes in the intensity of seedling defoliation associated with variation in vegetation structure have been documented elsewhere. Humphrey & Swaine (1997) found that *Q. robur* and *Q. petraea* seedlings were significantly more defoliated under the closed than under the open oak canopy or under canopies dominated by *Betula* spp. Riley & Jones (2003) found that seedlings of *Q. alba* presented more leaf herbivory in understorey plots than in adjacent clear-cuts.

The most likely explanation for the defoliation response recorded in this study is related to the life cycle of oak-specific herbivores. It has been documented that after emerging and feeding in the canopy, lepidopteran larvae frequently fall from the oak canopy and feed on oak seedlings before pupating in the forest floor (Humphrey & Swaine 1997; Wada *et al.* 2000), therefore seedlings growing near conspecific adults are likely to present more defoliation than seedlings growing further from the trees. Wada *et al*. (2000) found that after two years, all the seedlings of *Q. crispula* initially located within five metres from the oak trunk died due to high levels of defoliation (75-100% leaf area lost), while 75% of the seedlings located at a distance of 15-20 m survived and presented lower levels of damage (0-25% leaf area lost).

In this study, there were no significant differences between defoliation intensity in seedlings planted along the edge and the forest interior. It is important to note, however, that different defoliation responses may result when considering time as factor and not only the difference between the initial and the final condition. For instance, seedling defoliation by lepidopteran larvae is episodic and there is evidence that lepidopteran larvae fall mainly during spring (Wada *et al.* 2000), therefore it is possible that seedlings established in July presented higher defoliation at the beginning of the experiment, however the low leaf turnover recorded in seedlings growing within the forest compared with the seedlings growing in the grasslands resulted in higher leaf damage index at the end of the experiment. For instance, higher damage on the leaves may induce a higher leaf turnover, Wadell e*t al.* (2001) found that leaves of *Q. laevis* containing active leaf-mining beetles abscised earlier than leaves without active miners. Wold & Marquis (1997) found that *Q. alba* seedlings that presented higher defoliation in the first growing season presented less subsequent damage due to changes in the leaf composition, therefore further analysis of data from this experiment should be performed to detect changes in the defoliation patterns across time.

In this experiment, most of the seedlings growing in the grasslands renewed the damaged leaves and the new leaves remained with low defoliation levels by herbivores at the end of the study. Similarly, Quintana-Ascencio *et al.* (1992) found

that *Q. crispipilis* seedlings generally produced more leaves in open grasslands than those in shrublands or forested stands, and that after one year of being introduced, seedlings had replaced 90% of their leaves, however they did not record any significant difference in defoliation intensity between the forested and the open habitats. In this study, more seedlings planted in the hard edges compared with –24 m into the grassland, presented some defoliation (at least one leaf with defoliation) during the study period with respect to their original condition. However, defoliation intensity was not related to this spatial pattern, suggesting that several types of leaf insect eaters may be responsible for the different patterns of damage observed in this study.

Generally plants are able to compensate for moderate levels of defoliation, however there is a threshold where the negative effects of herbivores (such as loss of nutrients or loss of photosynthetic leaf area) will reduce growth and eventually may affect survival. In this study, even though a high proportion of the seedlings presented some level of defoliation, higher mortality was not directly related to higher herbivory damage in all the species tested. Similarly, *Q. crispipilis* seedlings and saplings transplanted in different successional stages presented herbivore damage of 10-20% of leaf area on <25-30% of each individual's total leaves, but this response was not related to mortality patterns between open areas and forested stands (Quintana-Ascencio *et al.* 1992). Moderate seedling defoliation by insects may play a negligible role in determining seedling survival (Adams & Rieske 2000): even after 75% defoliation, seedlings of *Q. liaotungensis* survived well until the end of the growing season, however complete defoliation caused seedling mortality (Li & Ma 2003).

The results presented here with respect to herbivore damage showed that insect herbivore damage patterns vary between species: most of the seedlings of *Q. laurina* and *Q. rugosa* presented defoliation but the leaf damage index was low. This pattern may result from many seedlings having few leaves damaged and low loss of leaf area. However *Q. segoviensis* and *Q. crassifolia* showed the opposite pattern, a low proportion of seedlings was damaged, but once at least one leaf was damaged, total damage to the plant was severe. *Q. candicans* seedlings presented intermediate

values in the frequency of the attack, renewed its damaged leaves during the experiment, and presented the lowest intensity of leaf damage. Similarly, species-specific defoliation responses have been reported by Dunning *et al.* (2003), who found that *Q. agrifolia* seedlings were preferred by insect leaf-eaters, which ate more leaf mass of this species than of *Q. engelmannii* seedlings. Differences between species may be determined by the preferences of the insects due to the different plant herbivore defences such as the concentration of allelochemicals, and by reducing the nutritional quality of their foliage (Wold & Marquis 1997).

Species-specific seedlings performance

Even though a high number of oak species coexist in the region of study (about 18 species; González-Espinosa *et al.* (1997)), there is lack of knowledge about the regeneration niches of oak species based on their physiological and adaptive strategies. Oak species differences in the region have been defined mainly by their local and regional distribution and abundance (González-Espinosa *et al.* 1997), altitude gradients (Alvarez-Moctezuma *et al.* 1999) and their presence and abundance in successional seres (Ramírez-Marcial *et al.* 2000). Although results from this ten-month experiment should be interpreted with caution due to unknown long-term responses, some important differences between the species tested may be discerned.

Contrary to my expectations, *Q. crassifolia* responded as a highly shade-intolerant species. Seedlings growing in the forested portion of the gradients in both edge types presented higher mortality rates, decreased its growth by diminishing the number of stems with respect to their original condition, higher loss of leaves and a higher proportion of seedlings scored as dead (which apparently were rotten). These responses may also indicate that seedlings of *Q. crassifolia* may have difficulties in acclimatising from the moderate light levels in the nursery to very low light levels. Similarly, Welander & Ottoson (1998) showed using shade houses that second-year seedlings of *Q. robur* decreased the number of leaves when the seedlings were transferred from a previous-year high light level to low light levels. It is possible that

Q. crassifolia seedlings were firstly affected by transplantation, were more susceptible to rot or herbivore attack and presented higher mortality within the forest and intermediate values along the edge.

Q. crassifolia seedlings transplanted from the nursery to high light conditions in the grasslands showed higher survival, increased the number of leaves, increased number of resprouts and shower greater accumulation of basal area. Similarly, new shoot production in oaks has been reported to increase as exposure to light increases (Harmer 1999). These responses to light conditions are typical from xerophytic oaks (*sensu* Larsen & Johnson 1998) that usually present a root collar with a large number of dormant buds, some of which activate upon the loss of the stem resulting in prolific sprouting as a response to disturbance or xeric conditions (Larsen & Johnson 1998). *Q. crassifolia* seedlings and saplings have been recorded growing in shrub and tree fallows after milpa cultivation (González-Espinosa *et al.* 1991) and this species is considered a component of oak and pine-oak forest (González-Espinosa *et al.* 1997). Park (2001) in a Mexican pine-oak forest found that regeneration of *Q. crassifolia* occurred (730 per ha) in steeper and more exposed slopes with a relatively open forest canopy, contrary to the patterns observed for other *Quercus* species.

According to my expectations, *Q. segoviensis* presented a more xeric-type response since the seedlings presented thinner stems (etiolation), higher leaf abscission and higher levels of defoliation along the forested portion of the gradient. Even though this combination of factors may affect seedling survival of *Q. segoviensis*, forest interior conditions were not detrimental to seedling survival during the experiment. However, further monitoring its necessary to detect possible changes in survival in the long term. *Q. segoviensis* is the only one of the five species tested that loses its leaves during the dry season as a response to moisture stress. There is a lack of information about the regeneration ecology of *Q. segoviensis* to compare with my results, however this species is distributed only from 2000-2500 m in the region, it is characteristic of exposed slopes, its abundance is moderate (Alvarez-Moctezuma *et al.* 1999) and its regeneration has been recorded within tree fallows (González-Espinosa *et al.* 1997).

In this study, oak species differ in basic seedling allometry and initial growth. Only *Q. laurina* seedlings allocated a relatively high proportion of carbohydrate to basal diameter during the experiment. *Q. laurina* and *Q. rugosa* presented relatively high seedling performance and greater plasticity in morphology that allowed these species to profit more from high light conditions and to survive well in low light conditions. Both species are highly abundant in the region at different altitudes. *Q. rugosa* is a very successful species able to colonise a variety of habitats, from xeric shrublands to humid sites, and presents a broad distribution both at a local scale (Park 2001) and at large scales (U.S.A, Mexico, Guatemala) (Zavala-Chavez 1998). *Q. laurina* is the main component of the canopy within the experimental forest stands, and may colonise open shrublands, pine dominated canopies (Camacho-Cruz *et al.* 2000) and old-growth forest (González-Espinosa *et al.* 1997). This species is able to persist under shade (Figueroa-Rangel & Olvera-Vargas 2000), and in other Mexican forest, *Q. laurina* has been recorded above 3500 m (Zavala-Chavez 1998). *Q. candicans* presented intermediate seedling responses, seedlings surviving equally well in the forested and the open portions of the gradient and also benefiting from the open part of the gradient. *Q. candicans* presents a distribution predominantly from 2000-2500 m, it has been recorded in pine and pine-oak forest, but not in tree fallows (González-Espinosa *et al.* 1997). It is more abundant in southern Mexico and Central America (Zavala-Chavez 1998).

Results of this study suggest that the species studied present seedling traits that are typical of early successional species in the study area. Care should be used in extrapolating these results for these species in xeric areas, where moisture stress may result in different patterns (Danner & Knapp 2003). For instance, Borchert *et al.* (1989) reported that seedling recruitment of *Q. douglasii* was positively associated with increasing cover and more mesic-sites at low elevations, but was negative with these factors at the cooler high elevations. In summary, in this study all the species showed better seeding performance in the open area of the forest-edge-grassland gradient, however *Q. rugosa* and *Q. laurina* were less affected by the forest interior conditions suggesting that they can persist under shade more readily than co-occurring congeners *Q. crassifolia* and *Q. segoviensis*. *Q. candicans* presented

intermediate values between the two types of seedling responses to the forest-edge-grassland gradient.

Soil moisture and rainfall patterns

In this study, soil moisture levels of shallow soils (4-6 cm) resulted in very homogeneous soil characteristics along the forest-edge-pasture gradient in both edge types (18-20%), suggesting that soil moisture was not a critical factor in the study sites. Soil moisture varied accordingly with the rainfall patterns, the period with lower rainfall (November to March) had the capacity to dry soils down to 35% of the soil moisture recorded in the rainy season. These changes may be responsible for the decrease in seedling survival recorded during May, especially in the case of *Q. crassifolia*.

Different early seedling responses due to species-specific timing of germination with respect to the rainfall patterns were not detected in this study. Germination of *Q. crassifolia, Q. rugosa* and *Q. segoviensis* occurs shortly after acorns drop in the autumn (September-November; Chapter 5), these species germinate and emerge during that period when rainfall is relatively abundant. Three or two-months old seedlings have to survive during the most severe drought period (December to March, Chapter 2). In the case of *Q. candicans*, seeds generally present dormancy for up to two months (Chapter 5), and natural seedling establishment of this species may occur during December to January, therefore this species has less exposure to the dry season (4 months). In the case of *Q. laurina*, dormancy of a proportion of acorns (up to 5 months) may result in seedlings being less exposed to the dry season and they may become established from January to April. In this study, after germination, seedlings were kept well watered in the nursery, therefore, interpretations about success in the natural establishment of this species should be made with caution.

Implications for oak expansion into the grasslands

From the general patterns recorded in this study it can be predicted that oak seedling performance is lower in the forest portion (including the forest edge) of the gradient than in the open area portion. Meiners *et al.* (2002) found that the probability of seedling establishment and the growth of *Q. palustris* in a temperate forest was higher as distance from the edge into the old-field increased, showing lower values in the forested portion of the gradient. Low light levels resulted in seedling etiolation which may act synergistically with higher leaf area losses, lower resprouting, lower leaf production and therefore reduced photosynthetic potential. Figueroa-Rangel & Olvera-Vargas (2000) in a mixed-oak forest in Manantlan, Mexico found that seedlings (<30 cm) of *Q. laurina* (1729 seedlings ha^{-1}), *Q. rugosa* (2625 seedlings ha^{-1}) and *Q. candicans* (812 seedlings ha^{-1}) were growing under an oak canopy with openness of 3-6%, however large seedlings were very infrequent, suggesting that most of these seedlings will not be able to survive the next year. This response may suggest that acorns at greater distances from the oak canopy have a higher probability of seedling establishment and underlines the importance of acorn dispersal to more suitable sites for seedling establishment.

In the study area, abandoned grasslands with shrub patches and a tall herbaceous stratum may provide appropriate sites for oak regeneration. Shrub cover near the edge may be particularly important if droughts are present (Danner & Knapp 2003). Previous studies have documented improved oak seedling survival (Li & Ma 2003; Gomez *et al.* 2003) and seedling growth (Callaway 1992) under shrubs, however this effect may be species-specific (Callaway 1992). Naturally established oak seedlings have been found more frequently under shrubs than in other microhabitats, in the case of *Q. douglassi* under *Salvia leucophylla* and *Artemisia californica* (Callaway 1992), *Q. humilis* under *Juniperus* sp. (Rousset & Lepart 2000) and *Q rugosa* and *Q. crassifolia* under *Bacharis vaccinioides* (Ramírez-Marcial *et al.* 1996). Rousset & Lepart (2002) found that the branches of unpalatable shrubs prevent sheep from gaining access to *Q. humilis* seedlings. Shrub facilitation may also be the result of an indirect effect: shrubs and tall herbs may inhibit the growth of other herbs or grass

species through allelopathy, shade and herbivory by small mammals that find a refuge under shrubs (Rousset & Lepart 2000).

If seedlings in mesic grasslands are protected from ungulates, herbivory of the roots is probably more likely to affect a proportion of seedlings in these habitats. About 13% of the seedlings that died 24 m into the grasslands crossing the hard edges showed evidence of root herbivory, suggesting that herbivores specialised in attacking the root system may be more frequent in the open grasslands than leaf eaters. Nevertheless, if large herbivores are suppressed, then any oak seedlings introduced would appear to be able to readily colonise open grasslands judging by the overall high seedling performance of all the species recorded in this study. Further research into the later phases of seedling establishment and sapling performance is needed since there is evidence that competition for resources may be more important as seedlings age (Crow 1988).

The variety of edge effects found in this experiment shows that the edge gradient determined by the edge type is not a uniform environment for tree recruitment and that oak species respond differently, mainly in response to variation in light availability. Results of this study and other studies in the region (González-Espinosa *et al.* 1991; Quintana-Ascencio *et al.* 1992; González-Espinosa *et al.* 1997) suggest that the regeneration of oaks could be accelerated if early-shrubby and mid successional communities in small clearings are more frequent in the forest mosaic than large open clearings and permanent grasslands. More extensive long-fallow (>25 years) Milpa agriculture and deferred rotational grazing would provide the heterogeneous landscape in the region beneficial for oak regeneration, especially for those species that are more shade intolerant.

CHAPTER 7: General discussion

QUESTIONS AND FINDINGS OF THIS STUDY

This study has three main findings: a) edge effects in forest mosaics had a significant effect on the regeneration processes studied, which occurred over small spatial and temporal scales, b) adjacent vegetation type not only affected the probabilities of tree invasion and regeneration, but also influenced edge effects within the forest interior and c) edge structure was linked to its function, tested in this study as the edge permeability of small mammals that are acorn predators and/or consumers. This study indicated that small mammals may exert a negative effect on acorn survival during a non-masting year, however during the mast-seeding year a proportion of acorns may survive. Analysis of tagged acorns showed that acorns were scatter-hoarded in sites appropriate for germination and seedling establishment.

The particular questions addressed in this study with a summary of the main related findings are summarised below:

1. **Are there differences in acorn removal across the forest-edge-grassland gradient and in each edge type?**
   Differences occurred, but these differences were recorded only within the open area of the forest-edge-grassland gradient. In hard edges there was a "matrix" type effect (very low acorn removal crossing the edge), whereas in the case of soft edges a "no edge" type response was recorded (similar acorn removal along the gradient). Comparing the two edge types (0 m mark) there was higher acorn removal in the soft edge compared with the hard edge.

2. **How is the edge permeability to acorn dispersers linked to the edge structure?**
   Peromyscus species were thought to be the main acorn predators and/or dispersers and their distribution was linked to the forested part of the gradient. However, 29 individuals of *Peromyscus* species were found in

abandoned grasslands crossing soft edges, whereas only two animals were recorded in the open grasslands near hard edges during the non-mast seeding year. The experiment using tagged acorns supported the hypothesis of high edge permeability in soft edges but low permeability in hard edges. Therefore, it can be suggested that as structural similarity of the vegetation at the soil level increases between two adjacent areas the permeability of edges to small mammals that are acorn consumers increase.

3. **Is masting by oaks determining different spatial and temporal patterns in acorn removal by small mammals on the ground?**
   Yes, but masting affected only temporal patterns of acorn removal (but see Question 4). Mast-seeding years are an important factor determining the intensity of acorn removal; a predator satiation mechanism operated during the year that presented low abundance of small mammals and a huge abundance of acorns, whereas the followed year higher and faster removal of acorns was recorded due to higher small mammal populations and lower abundance of acorns. The spatial differences of acorn removal between edge types along the forest-edge-grassland gradient were similar in both years (Chapter 3).

4. **Is the adjacent land use affecting distance-from the edge related acorn removal patterns within the forest interior?**
   Yes, but this effect was only significant during the non-masting year (Chapter 4). More acorn removal by arboreal small mammals was recorded near the hard edges contrary to my expectations. However, during the mast-seeding year no significant differences were recorded. This different response suggests that mast-seeding years are affecting the spatial patterns of acorn removal, probably by changing not only the abundance but also the composition and the foraging behaviour of small mammal communities.

5. **Do oak species with different timing of germination have different probabilities of being removed?**

   Yes, according to the results of the mast-seeding year, acorns near germination were consumed *in situ* and acorns with dormancy were left intact, using the experiment dishes as a cache (apparently by squirrels). During the non-masting year acorns of both types were readily and equally removed and no significant differences were recorded. Also there was a confounding effect of the size of the acorns that were exposed to predators, therefore this question is partly explained by the results of this study. More research is needed that controls acorn size and uses selective access to the dishes in order to identify how particular predators may change their abundance and behaviour during mast seeding and non-mast seeding years.

6. **How do different habitats (forest, edge and grassland), in both edge types, affect acorn germination?**

   Total acorn germination was generally higher in the grasslands of both edge types, however more acorns developed into seedlings at the edge in the soft edges than in the hard edges. More non-germinating acorns became rotten in the edge and in the forest in sites with soft edges than in the same positions in sites with hard edges, suggesting that even though soil moisture did not differ significantly between habitats, differences between edge types may affect the acorn moisture availability. Germinating acorns in grasslands, especially in those grasslands in sites with soft edges, received lower insect damage than acorns in the edge and in the forest.

7. **Are there differences in acorn germination timing between species belonging to different subgenera?**

   Yes, however, even though *Q. crassifolia* belongs to the red oak group (as *Q. laurina* and *Q. candicans*), it presented the faster germination rate contrary to what has been reported as typical for red oaks in temperate areas. The laboratory experiment showed that all the species presented different germination curves across time and results in the field showed that after 73

days, *Q. laurina* presented lower values of germination but a higher proportion of apparently viable acorns than *Q. rugosa,* which produced most seedlings in the same period of time. *Q. crassifolia* presented the lowest germination in both the laboratory and the field experiment, however this result has to be interpreted with caution since the acorns may have been affected by cold storage before the experiments began.

8. **To what extent does the presence of the leaf litter cover in each spatial position affect acorn germination?**

   Vegetation cover can increase acorn germination, but in this study was important only when the substrate did not allow acorns to become covered, as in the case of microhabitats in the open areas of sites with soft edges. When acorns were covered by the existing heterogeneous substrata and additional cover was placed above them, a negative effect was recorded due to more exposure to rot or pathogen attack, as was recorded for *Q. crassifolia* acorns. Therefore, the positive effect of litter cover can be microsite- and species-specific.

9. **How does the structure of the vegetation across forest-edge-grassland gradients in each edge type affect seedling establishment and the incidence of seedling predation?**

   In general seedling survival and growth were higher along the open area of the forest-edge-grassland gradient. Seedlings were less predated in the grasslands than in the forest and presented intermediate values in the edge. However higher seedling survival and growth rates in stem height were recorded along the grasslands of sites with soft edges, particularly 12 m from the edge into the grassland. This underlines the positive effect of intermediate shade on oak seedling performance.

10. **Are there differences in the seedling performance between species?**

    Species differed in their initial seedling allometry at the beginning of the experiment. *Q. crassifolia,* contrary to expectations, presented a highly shade

intolerant response and was the most affected by the forest interior conditions, as seedlings presented significantly lower survival within the forest than in the open habitats. All the species presented higher seedling performance in the open area of the gradient; surprisingly *Q. candicans* presented higher performance in the grasslands. General seedling performance patterns were recorded between species ordered as follows: *Q. rugosa*>*Q. laurina*>*Q. candicans*>*Q. segoviensis*>*Q. crassifolia*. Interestingly the species presented different resprouting abilities, new stem production was recorded ordered as follows: *Q. crassifolia*>*Q. laurina*>*Q. rugosa*>*Q. segoviensis*. *Q. candicans* did not produce more than one stem. Species presented different susceptibilities to insect damage and different leaf turnovers to compensate for leaf damage.

NET EDGE EFFECTS ON OAK REGENERATION

Spatial and temporal seed-seedlings conflicts

Seed-seedling conflicts in plants occur when conditions that are advantageous for one plant development stage are disadvantageous for another (Schupp 1990; Kollmann & Schill 1996; Fuchs & Krannitz 2000). Schupp (1995) has reviewed these relations and stated that the most critical plant life stages, seed survival, germination and seedling establishment, might follow fully discordant patterns in the same microsite. He stated that the common feature in the examples that he presented is that the characteristics of a patch type that make it highly suitable for germination and seedling growth, make it unsuitable for escape from seed predators. However, he has not considered the potential positive effects that small mammals have on seeds, especially when he refers to the available information for *Quercus* species and predation by squirrels and small mammals. Even today many authors equate seed removal to seed predation (Borchert *et al.* 1989; Callaway 1992; Crawley & Long 1995; Herrera 1995; Hau 1997; Diaz *et al.* 1999; Lehtonen *et al.* 2001; Plucinski & Hunter 2002), but growing evidence suggest that this is a misconception (Jensen & Nielsen 1986; Kikuzawa 1988; Miyaki & Kikuzawa 1988; Forget 1996; Steele *et al.*

2001; Steele & Smallwood 2002; Jansen 2003) and that temporal variability in seed production and seed differences between species may lead to different patterns of seed survival (Chapter 3 and 4). The occurrence of mast-seeding years determines whether acorn removal may lead to dispersal or predation. Jansen (2003) documented that during the mast-seeding year, potential recruitment of a neotropical nut-bearing tree (*Carapa procera*) was 15% of the caches by small mammals and during a poor year this proportion decreased to 3%.

There is no information available about the frequency of mast-seeding years, nor about synchronicity in acorn production between oak species in the study area. My observations are that for some species such as *Q. rugosa* and *Q. laurina*, mast seeding years may occur every two years, and for others such as *Q. crassifolia*, *Q. segoviensis* and *Q. candicans* the pattern of bearing fruit is not clear. During the mast-seeding year recorded in this study, all these species showed high acorn production in the study area and nearby areas. However, acorn production of species such as *Q. crispipilis* was not synchronised with the rest of the species, suggesting that there may be alternate-years bearing at the region level. Acorn production also varied considerably among individual trees within a year, and trees with poor acorn production were observed even in the mast-seeding year (pers. obs.). The consequences of synchronicity or alternate-year bearing between coexisting species have not been studied, but will influence probabilities of oak regeneration and will also affect other components of the forest community (Schnurr *et al.* 2002). During a mast-seeding event, populations of acorn consumers increase the following year. Oak species that are not canopy dominants and that present isolated mast events under these conditions will have high acorn predation and predator satiation will not operate. A trend towards synchronicity of masting between several tree species has been considered as an evolutionary adaptation to seed predator satiation; for instance, reproductive synchrony of 48 dipterocarp species has been documented as a response to pre- and post-dispersal predation (Curran *et al.* 1999; Curran & Leighton 2000).

Oak recruitment is influenced by a complex of many factors. In order to simplify the patterns found in this study and predict net effects (predicted recruitment) on oak

regeneration in a qualitative manner, I summarise on Table 7.1 the influence of the studied processes on the potential outcome in oak recruitment in each habitat type (forest, edge and grasslands) in each edge type (hard and soft) and in each year (mast seeding year and non-mast seeding year). The assigned value (high, medium or low) in each process (acorn removal, seedling emergence and seedling performance) is relative to the other habitats in the same row (i.e. forest vs. edge vs. grassland). The outcome was obtained by considering the value of each process in each habitat (columns). The outcome of the balance of these discordant probabilities may determine the effectiveness of oak dispersal across edges and adjoining old-fields.

Table 7.1 General outcomes of the oak regeneration process obtained in this study and the hypothesised net effects in accordance with the occurrence of mast seeding and non-mast seeding years. This model assumes that from year to year there is no variation in the acorn germination and seedling performance patterns and that the occurrence of mast seeding years only affects the probability of acorn dispersal and survival in each habitat. Therefore the balance may shift from negative to positive in acorn removal during years with high abundance of acorns.

A) NON-MASTING YEAR: HARD EDGES			
Processes	**Forest**	**Edge**	**Grassland**
Removal	High	High	Low
Seedling emergence	High	Medium	High
Seedling performance	Low	Low	High
Predicted recruitment	VERY LOW	VERY LOW	SEED LIMITATION
B) MASTING YEAR: HARD EDGES			
Processes	**Forest**	**Edge**	**Grassland**
Removal	High	High	Low
Seedling emergence	High	Medium	High
Seedling performance	Low	Low	High
Predicted recruitment	MEDIUM	MEDIUM	SEED LIMITATION
C) NON-MASTING YEAR: SOFT EDGES			
Processes	**Forest**	**Edge**	**Grassland**
Removal	High	High	High
Seedling emergence	Low	Medium	High
Seedling performance	Low	Low	High
Predicted recruitment	VERY LOW	VERY LOW	VERY LOW
D) MASTING YEAR: SOFT EDGES			
Processes	**Forest**	**Edge**	**Grassland**
Removal	High	High	High
Seedling emergence	Low	Medium	High
Seedling performance	Low	Low	High
Predicted recruitment	LOW	MEDIUM	HIGH

From the results of this research, abandoned grasslands crossing soft edges represent the regeneration "window" for oak species but only during the mast seeding years (Table 7.1d). Callaway (1992) suggested that shrublands seem to be suitable sites for germination, and growth of *Q. douglassi*, however small mammals that are also acorn predators do best in these habitats leading to discordant patterns of patch suitability. Similar patterns in abandoned grasslands were recorded in this study, but are interpreted differently (Table 7.1d). I believe that higher seed removal in these sites may reflect higher small mammal activity. Under low population density and high abundance of resources, small mammals may potentially also disperse single acorns covered by leaf litter to these sites (Chapter 3), resulting in higher levels of germination (Chapter 5) and seedling establishment (Chapter 6) and lower levels of insect damage (Chapters 5 and 6). Similarly, Quintana-Ascencio *et al*. (1992) found higher acorn removal but also higher establishment of *Q. crispipilis* saplings in early successional shrub-dominated stands that are more protected against injury by livestock, and at the same time are exposed to intermediate light conditions.

Similar to the results of the current research, previous studies have shown that open grasslands present low acorn removal (Quintana-Ascencio *et al.* 1992; Callaway 1992), which reflects low activity of acorn consumers (Chapter 3). Therefore in open grasslands it can be assumed that there is a seed limitation factor (Table 7.1a and b), suggesting that in the study area oak colonisation into open grasslands (sites with hard edges) is suppressed by low acorn availability because acorn predators and/or dispersers (*Peromyscus* spp.) fail to cross far into these habitats (Chapter 3). Various studies have documented seed availability as a major limiting factor in forest recovery on abandoned pastures (Widjeven & Kuzee 2000). I have not observed jays caching acorns in open grasslands as has been documented in previous studies in temperate forests (Kollmann & Schill 1996; Hubbard & McPherson 1999). Jays are hunted in the study area and this may change their foraging behaviour in open habitats. In the grasslands in sites with hard edges, I recorded high levels of germination and seedling survival, however, protection from large herbivores was used in both open grasslands and abandoned grasslands. In these habitats early establishment of seedlings may be limited by browsing by ungulates. Quintana-

Ascencio *et al*. (1992) found that in grassy habitats, low acorn availability and browsing and trampling by ungulates arrest the establishment of *Q. crispipilis*.

Although oak seedlings resprout after foliage removal, continued defoliation may result in a cycle of production of new leaves and resprouting (Rousset & Lepart 2000), resulting in highly branched plants that may survive for many years, but they never achieve reproductive size or a threshold height where saplings are no longer available to herbivores. Seedlings under these conditions are thought to be less competitive with other plants or grasses and may eventually be killed by moisture or drought stress (Collet *et al.* 1996).

From the results of this study, during the mast-seeding year oak regeneration at the edge (0 m mark) may be intermediate with respect to the forest-edge-grassland gradient, (Table 7.1b and d). I found a positive effect of the edge on oak regeneration due to higher germination and seedling emergence and less insect damage on acorns compared with the forest interior, but also higher activity of acorn consumers (Chapter 3), especially during the non-mast seeding year (Chapter 4). Therefore it is expected that in years of high abundance of acorns and low abundance of small mammals the edges may function as regeneration sites of oaks. Similarly, Bonfil & Soberon (1999) found higher acorn removal rates at the forest edge but also high germination and seedling establishment rates.

Comparisons of the same habitat types in sites with hard and soft edges are presented in Table 7.2. Soft edges presented higher acorn removal, which may represent in years of low acorn abundance a negative effect, but a positive effect in the case of mast seeding years. There were more seedlings emerging in the forest of sites with hard edges compared to sites with soft edges, suggesting that edge structure is also affecting regeneration processes within the forest, as was also shown with data of acorn removal by arboreal rodents (Chapter 4). Forest patches adjacent to intensively used grasslands present an understorey more disturbed than forest patches adjacent to abandoned clearings. This is due to browsing within the forest and forest edge by livestock and higher activity of the farmers within these forest patches.

Table 7. 2 Comparisons between sites with hard and soft edges along each habitat (forest, edge and grassland) for each of the studied regeneration processes.

	FOREST		EDGE		GRASSLAND	
Processes	**HARD**	**SOFT**	**HARD**	**SOFT**	**HARD**	**SOFT**
Removal	High	High	Low	High	Low	High
Seedling emergence	High	Low	Low	High	High	High
Seedling performance	Low	Low	Low	Low	Low	High
Predicted recruitment *	HIGH	LOW	LOW	HIGH	LOW	HIGH

* During the mast-seeding year.

Once the clearing is abandoned, a process of succession from abandoned grasslands to shrublands or secondary forests may take place at the forest edge and the edge may change its position as time proceeds. Oosterhoon & Kappelle (2000) documented that the invasion of *Myrsine coriaceae* (pioneer species) into the forest and grassland edge may facilitate the further invasion of *Q. copeyensis* and therefore a fast encroachment of secondary vegetation may lead to secondary oak forest within a 25-35 year period. In this study, a facilitation effect not only of shrubby vegetation, but also from tall herbaceous strata was recorded by allowing activity of small mammals and providing appropriate microsites for oak seedling establishment. Shrub vegetation bordering forest patches may result in subsequent competition between oaks and shrubs communities and create borders that change temporally and spatially.

The present study focused in how processes occurring at small temporal and spatial scales were affected by the present forest and clearing structure, however all the sites presented high variability in their land use, age and floristic composition. It was difficult to make inferences about successional pathways because clearings have never been completely abandoned since last Milpa cultivation. However, the results presented here may be useful to explain some of the observed successional pathways and floristic changes observed in chronosequences after Milpa cultivation in similar oak montane forests. Further research will be necessary to include different successional seres as clearings in advanced successional stages as early successional forest adjacent to mature forest resulting in older edges.

As shown by this study, studies focusing only on a single recruitment process such as seed removal and undertaken in only one year, may give misleading predictions about oak regeneration. In addition, the relative importance of the factors affecting oak regeneration along forest-edge-pasture gradients may vary both spatially and temporally. Habitat quality may be highly dynamic as the oaks continue to grow, and factors such as densities of acorn predators and seedling herbivores can also change as oaks reach different developmental stages. As documented in this study, fungal and insect populations affected acorn and seedling survival, therefore their distribution and composition along the forest-edge-grassland gradient should be evaluated in future studies.

Previous research has documented that soil nutrients and light availability becomes more important factors as seedlings ages, due to seedling dependence on the cotyledons. Most of the first year seedlings under dense canopy cover rely on the cotyledons reserve, but once they are depleted they growth and survival rate decreases with prolonged exposure to shade (Crow 1988; Welander & Ottosson 1998; Guo *et al.* 2001; Collins & Battaglia 2002). For further research it is recommended that along the forest-edge-grassland gradient other microsite variables should be estimated in addition to the light environment such as soil humidity (soil water potential) and nutrients available to the plants (as nitrogen, phosphorus and calcium) that may affect late oak seedling and sapling establishment. Also the litter conditions and humidity aboveground may affect acorn germination. Litter depth and litter type may affect the behaviour and activity of small mammals and therefore affect cache microsite characteristics and therefore acorn germination.

In this study, physiological responses and dry mass allocation were not evaluated, which constrained the interpretation of the observed patterns of seedling performance. To evaluate the magnitude of the factors affecting seedling establishment along the forest-edge-grassland gradients, it will be necessary to estimate variables such as above- and below-ground dry mass allocation, leaf area ratio, photosynthetic light response of the different seedling species and evapo-transpiration rates. As root infection seems to be an important factor affecting oak

seedling survival within the forest and its effects are related to the water status of the plants, measurements of leaf water potential and stomatal conductance may also be useful (Robin *et al.* 2001).

Competition with shrubs and herbaceous species may restrict sapling survival and growth in the open area of the gradient, therefore shoot extension may be important in competition for light between the tree seedlings and the surrounding vegetation. The observed growth allocation to stem in soft edges in this study (Chapter 6) may promote seedling survival if overtopped by a tall herbaceous or shrub stratum, and will eventually protect also seedlings from herbivory. Once the shrub canopy and the tall herbaceous stratum have been overtopped, *Quercus* saplings will continue to develop and their survival would no longer be threatened by grazing. Previous investigations of secondary succession in the study area suggest that the shade tolerance of *Quercus* species may contribute to their ability to eventually replace the shrubs under which they are established (González-Espinosa *et al.* 1991; Ramírez-Marcial *et al.* 1996).

Oak dispersal and current fragmentation patterns

Oaks fail to replace themselves *in situ*, relying in the chance that acorns will be dispersed to openings for establishment. In this study the main advantage of oak dispersal into grasslands seems to agree with both the escape hypothesis (to escape from a disproportionate mortality near parent plants) and the direct dispersal hypothesis (dispersal agents take seeds to non-random places that are well suited for establishment and growth) (Howe & Smallwood 1982). *Quercus* invasion into abandoned grasslands may occur at rates that depend on a) the occurrence of mast seeding years, b) fluctuations of small mammal populations and c) mobility of acorn dispersers determined by the edge type. The occurrence of these processes may be highly affected by current forest fragmentation patterns in the study area as described below:

A) Mast seeding years and predator satiation represent a reproductive strategy particularly vulnerable to disruption (Curran *et al.* 1999). Acorn production patterns can be affected by the human use of oaks in the area and habitat fragmentation patterns. Continued cutting of branches of small trees for fuelwood may retard or inhibit the occurrences of reproductive events (González-Espinosa *et al.* 1995). Fragmentation resulting in isolated populations of wind-pollinated trees such as oaks may decrease reproduction and therefore acorn production. Although oaks are monoecious, oaks are mostly outcrossing and self-pollination is thought to be prevented by gametophytic self-incompatibility (Sharp & Sprague 1967). Knapp *et al.* (2001) studied fragmented stands of *Q. douglasii*, and found that acorn production was positively associated with the number of pollen-producing neighbours and this relation was stronger when neighbourhood sizes of 60 m or larger were taken into account. Considering these results, a low density of reproductive oak trees due to thinning, clearing and firewood harvest together with isolation of forest fragments is likely to alter the spatial structure of oak populations and interfere with reproduction and acorn production. Santos & Telleria (1997) found that in a highly fragmented landscape large acorn production occurred only twice in seven years, resulting in high acorn predation, especially in small fragments. Curran *et al.* (1999) documented that predator satiation occurs at a landscape level rather than within local stands; without sufficient quantity and spatial extent of seed production, nomadic and resident predators and or dispersers in forest fragments may destroy all seed produced in a local stand. If remaining oak trees in isolated and small forest patches in the study area produce fewer acorns or present asynchronous fruiting, the potential for oak regeneration will be very low, and considering the importance of acorns in the entire forest ecosystem, lower acorn production may decrease the occurrence of several species of animals and affect the regeneration of other forest tree species.

B) Fluctuations of small mammals populations. There is a lack of long-term studies about the fragmentation and disturbance effects on small mammal

populations in the Highlands of Chiapas. Horvarth *et al.* (2001) documented higher diversity of small mammals and different species composition within a pine-oak-*Liquidambar* forest in Chiapas when compared with agricultural lands. Fragmentation patterns in the study area have resulted in development of several isolated small forest fragments (Ochoa-Gaona 2001). Studies of the habitat islands in small mammals have documented that, at some threshold value, forest patch size and degree of isolation of the original habitat will begin to influence the population size of animals. Population isolation increases the probability of extinction due to factors such as stochastic demographic and environmental variation and inbreeding depression (Turner 1996). One of the short-term consequences of forest isolation on small mammal populations is the decrease in emigration, and low emigration may lead to a population increase (Kozakiewicz 1993). The consequences of an increased population of small mammals in isolated fragments may exert a negative impact on seeds or seedlings (Ostfeld *et al.* 1997). Santos & Telleria (1997) found higher acorn predation by mice in small forest fragments compared with large forest fragments due to higher concentrations of small mammals. Predator satiation may not work under these conditions. Gomez *et al.* (2003) found during the mast-seeding year that *Q. pyrenaica* acorns were all consumed *in situ* and introduced seedlings suffered damage by mice and ungulates and none of the seedlings survived. This may be attributable to the fragmentation patterns and the unusual abundance of predators and/or dispersers.

C) Mobility of dispersers. Small-scale forest mosaics with shrub and tree fallows and low scale disturbance may enhance mobility of acorn dispersers across the matrix as has been shown in this study. Similarly mobility of small mammals may be enhanced in small-scale forest mosaics (Andren 1994; Bayne & Hobson 1998; Hovland *et al.* 1999; Rodriguez & Andren 1999). At present, forest fragments in the Highlands present an intermediate contrast with adjacent areas, which means that secondary forest or agricultural abandoned lands surround at least part of the forest fragments (Ochoa-Gaona

2001; Ochoa-Gaona *et al.* 2003). In some areas current land use in the Highlands of Chiapas is altering the spatial arrangement of the landscape, leading to large and intensively used open patches that represent barriers to the movement of small mammals confined in small forest patches. Small mammals that are forest specialists may then fail to cross open areas with homogeneous vegetation due to the higher visibility of predators and the higher risk of being discovered (Mills 1995). Small mammals may also change their foraging and dispersal behaviour due to fragmentation (Bowers & Dooley 1993; Kotler *et al.* 2001; Anderson & Boutin 2002), for instance, animals capable of dispersing large seeds will not cross certain open habitats or when they do, it is unlikely that they will do so carrying large seeds because they will have less opportunity to react if a danger of predation occurs (Wunderle 1997).

Despite the fact that the Highland forests have been used for centuries, it appears that plant species have not gone locally extinct, however the species richness and abundance of animals in these perturbed areas have been altered. In the long term local extinction of animal dispersers will have an impact on entire forest systems (Dirzo & Miranda 1990). Ochoa-Gaona *et al.* (2003) recorded in the Highlands of Chiapas that richness of shrub species was affected by forest isolation and the number of shrub species decreased as the fragment shape complexity increased (more edge-area ratio). This pattern may be related to the defaunation and forest isolation processes, as a high proportion of shrubs species in the area have animal-dispersed seeds. The challenge in these systems is to identify the thresholds in fragment size, matrix composition, degree of isolation and distance to the source where the occurrence of vertebrates and the probability of oak expansion and forest regeneration diminish.

Restoration of montane forests

Small-sized clearings, moderate land use intensity, and a fine-scaled forest mosaic may result in higher seed inputs, and potentially increase the rate of forest recovery

(Myster & Sarmiento 1998). It has been suggested that in highly fragmented landscapes the spatial arrangement of habitat patches becomes very important for the maintenance of the high biodiversity (Andren 1994). Williams-Linera *et al*. (1998) found in a Mexican tropical rainforest that the heterogeneity of landscape features (forest edges, riparian sites and isolated trees) provided regeneration sites for primary species and that the preservation of this heterogeneity maintained high plant species diversity. In human-created landscapes, intermediate heterogeneity may maintain high biodiversity, but there is a threshold in the scale of this heterogeneity where the patches are no longer suitable and the balance between human disturbance and natural regeneration is lost. This study showed that by maintaining more soft edges and a small-scale fragmentation enhancing shrub communities in the clearings, natural regeneration of oaks is achievable. However, current trends in landscape use patterns point to a progressive forest deterioration; forest recovery of large and severely degraded sites and open grasslands surrounded by degraded forest or other agricultural lands will take a considerable period of time, therefore, forest restoration and rehabilitation may be regarded as valuable options (Twedt & Wilson 2002).

If forest recovery is seriously hindered due to the limited availability of seeds, a restoration strategy could include the introduction of seedlings during the rainy season into early successional stages following abandonment of agriculture, protected from livestock. In this study, the effect of mycorrhizas on seedling establishment was not evaluated. However, previous research has indicated that mycorrhizas have a significant role in oak seedling establishment (Rieske 2002), especially when seedlings are growing in poor soils or in habitats where seedlings must establish quickly to survive (Perry *et al.* 1987). Clear cutting usually results in reduced mycorrhiza formation, particularly when the clearing is continually used (such as permanent grassland) and no other host plants are present to maintain fungal populations (Zhou *et al.* 1997). In this study, seedlings were planted in the forest-edge-grassland gradients using forest soil from the study area; this indigenous soil may enhance root colonisation by natural populations of mycorrhizal fungi. In order to generate successful restoration practices, long-term research is needed to evaluate the performance of seedlings planted in the grasslands with mycorrhizal fungi and

forest soils versus direct seeding of acorns, in order to evaluate the role of mycorrhizas and the effect of introducing oaks at different developmental stages.

The maintenance of isolated trees of species such as oaks in the grasslands and crops is also very important. Although not measured in this study, trees in open areas produced large amounts of acorns in both years and if cattle and agricultural practices are excluded, isolated trees could effectively act as regeneration nuclei (Williams-Linera *et al.* 1998). As oak populations consist of trees ranging from low to high fruiting potential, a feasible practice is the selection and marking of individual trees that are good acorn producers in order to protect and use them as a seed source for restoration programmes.

Another strategy is to enhance shrubs in recently abandoned Milpas by planting them or sowing their seeds. Shrubs may function as a nurse to facilitate the posterior introduction of intermediate- and late-successional tree species. The successional role of shrublands as a tool for vegetation management has been documented previously. Ramírez-Marcial *et al.* (1996, 1998) found a facilitation effect of *Baccharis* shrubs on pine and oak seedlings and recorded the presence of four species of canopy trees and five understorey species in shrublands that are surrounded by mature forest.

This study contributed to the understanding of the factors determining oak tree establishment, which is critical to predicting the results of tropical montane forest restoration efforts. The generality of the conclusions reached in the present study await further multiyear analysis of the dynamics of seedling and sapling recruitment along the forest-edge-grassland gradient. Management techniques such as sealing of the edge can be promoted by planting native shrubs, vines, or understorey trees, this will help to ameliorate the edge effects within the forest (i.e. nest predation; Fleming & Giuliano 1998) and also may function as a live fence to avoid the entrance of livestock that browse the tree seedlings that may be more abundant in the forest edge. Shrubs in the edge may promote a dynamic edge that changes in space and in time, which will enhance forest recovery and will provide more suitable wildlife habitat.

PERSPECTIVES FOR FUTURE STUDIES

Edge effect studies and experimental design considerations

To understand the effects of habitat fragmentation it is essential to specify the scale of habitat fragmentation, which is related to area requirements of individuals, home range boundaries and movement patterns of individuals (Andren 1994). This study was performed in a small area within a forest mosaic. This may constrain the scaling up of the edge effects recorded in this study (Manson 2000). The fact that each site represented one edge type makes it difficult to test the site effect. For future experimental designs it is recommended to have different edge types in the same clearing. For instance, use large and abandoned clearings within the forest and manipulate part of the vegetation in order to see how vegetation structure at different spatial scales affects edge permeability.

Habitat patches are parts of a landscape mosaic and the presence of a given species may be a function not only of a patch size and isolation, but also of the kind and suitability of neighbouring habitat (Andren 1994). By comparing different landscapes as forest mosaics vs. intensively fragmented areas and performing cross-scale edge studies it would be possible to determine whether these edge effects are scale-dependent (Donovan *et al.* 1997). Quality of edges and not only quantity should be considered when fragmentation patterns are interpreted. For instance, edge effects may be more severe in forest mosaics than in relatively homogeneous forests because the edge effect at any point is a function of the nearest edge (Malcolm 1994), however if there is larger edge length with lower contrast or abruptness this may have less negative effects on the forest patches than lower edge length with high contrast or hard edges in a relatively continuous forest.

It is clear from this research that instead of investigating simplistic and descriptive patterns due to the edge presence within the forest, one may also test mechanistic hypotheses in order to relate vegetation structure to function and discover how both habitats interact. By long term monitoring of masting patterns or by manipulating the

ambient food availability, different spatial patterns of regeneration processes such as predation may be recorded at the edge (Conner & Perkins 2003). Future studies of edge effects should include the temporal variation of the processes and enough information about landscape variables (fragment size, shape, isolation, contrast) to conduct a comprehensive analysis of the consequences of fragmentation on the ecological processes.

Animal-acorn interactions

Although the effect of insects on acorn survival was not deeply studied in this dissertation, results from this study and previous research has shown that the effect of various insects guilds on acorns and seedlings is complex and varies spatially and temporally (Stork *et al.* 2001; Fukumoto & Kajimura 2002; Yu *et al.* 2003). Also, different intensities of acorn damage have an impact on further stages in oak development (Andersson 1992; Branco *et al.* 2002). In Chapter 5, germinating and non-germinating acorns presented damage by insects, but patterns were different in each habitat and habitat edges presented intermediate values compared to the forest and the grassland. Further research should document how composition and abundance of insects that rely on acorns vary spatially in the forest-edge-grassland gradient and how this may affect acorn fate and seedling performance.

Further research is needed to determine the interactions between jays and acorn dispersal in fragmented montane forests. Several studies in temperate regions have indicated the importance of jays as long-distance (up to several kilometres) oak dispersal agents (Bossema 1979; Darley-Hill & Johnson 1981). Forest edges seem to affect the acorn caching behaviour and abundance of jays (Kristan III *et al.* 2003). Johnson *et al.* (1997) found that jays tend to cache more acorns under the litter cover in edges than in grasslands or open areas. The relative importance of birds as long distance (often >1 km) dispersal agents compared with short-distance dispersers (<150 m) of oaks is probably greater in highly fragmented landscapes and in forest mosaics with hard edges. Therefore information about their contribution to oak

dispersal in fragmented landscapes is very important in order to predict natural oak regeneration.

The occurrence of natural disturbances such as landslides and windstorms in the study area may also act as oak dispersal mechanisms interacting with the effect of animal dispersal. For instance, it is possible that slope wash over very steep slopes may move acorns downhill and disperse them across the forest edges or open areas. Once moved, acorns may be exposed to secondary dispersal by animals. Fruiting oak trees that fall due to occasional but severe windstorms in the study area may also alter acorn distribution and abundance and contribute to oak dispersal. That could have happened in 1982 when a severe windstorm in the study area opened the canopy of the mature oak forest stands (González-Espinosa *et al.* 1991). The relative importance of these mechanisms through time and space is unknown, though they are likely to be relatively rare events. More research is needed to determine if these are periodic natural disturbances and if they are positively or negatively related to oak expansion into open areas.

The high oak diversity in the region suggests that enormous potential still exists for clarifying the mechanisms involved in allowing coexistence and resulting in different dominance patterns of the species. Species present different acorn sizes, shapes, pericarps, germination schedules, composition and distribution of various chemical compounds (such as tannins). All these acorn characteristics are known to affect the manipulation of acorns as food storage by small mammals resulting in different probabilities of dispersal (Steele *et al.* 2001) and different dispersal distances (Smallwood *et al.* 1998). Further research should consider tagging acorns of different species, exposing them to selected predators (using enclosures) and determine their final fates (Steele *et al.* 2001) during mast-seeding and non-masting years.

Even though there is strong evidence that acorns represent a very important food resource for small populations and acorn abundance will determine their fluctuations in size (Margaletic *et al.* 2002), the role of acorn tannins in food preferences of rodents is highly questionable. Indeed, Shimada & Saitoh (2003) showed that the

tannins could cause serious damage to mice; when captive animals are maintained eating only acorns, mice die due to body weight loss and negative nitrogen digestibility. A plausible hypothesis for explaining how mice could overcome the negative tannin effects may be related to the gradual intake of tannins in natural conditions, or the presence of weevils in the acorns as a source of protein that may neutralise body weight loss. But there is need for research to reveal these complex mechanisms and their consequences for acorn survival. Several multi-trophic interactions have been suggested in the literature that involved acorns and: a) small mammals and weevils (Steele *et al.* 1996), b) jays and weevils (Hubbard & McPherson 1997) and c) moths, mice and deer populations (Ostfeld *et al.* 1996; Elkinton *et al.* 1996).

Fig. 7.1 *Curculio* sp. an acorn weevil. Photo by H.A. Turney.

Acorns represent a key element of the ecosystem; several species rely on the occurrence of acorns (e.g. more than 150 species of birds and mammals in North America) (Steele & Smallwood 2002). There is a lack of information about how these complex and unstable interactions are affected by human disturbance and

landscape fragmentation. There are many questions to answer, but unless these montane forests are preserved and restored, current conversion rates will cause the loss of high biodiversity before we discover their complex interactions. We must increase our efforts to implement sound practices that create a balance between the basic requirements of communities living within the region and the conservation of these unique ecosystems.

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Appendix 1: Chapter 2

Table A.1.1 Relative importance values (RIV) for each species (small saplings, large saplings and trees) along the grassland-edge-forest gradient (plots at different positions from the edge). Negative distances indicate metres into the grassland and positive number indicate metres into the forest from the edge. The importance values (%) were calculated for each species considering the number of stems, accumulated basal area and frequency in each plot along the grassland-edge-forest gradient.

			Grassland		Forest					
Species	**Family**	**Status**	**-10-20**	**-10-0**	**0-10**	**10-20**	**20-30**	**30-40**	**40-50**	**50-60**
Alnus acuminata ssp. arguta (Schldl.) Furlow	Betulaceae	Early	37.3	7.3	5.4	0.5	0.3			
Arbutus xalapensis H.B.K.	Ericaceae	Early			0.4					
Archibaccharis asperifolia Benth.	Asteraceae	Mid					0.3			
Buddleia americana L.	Loganiaceae	Early			0.4	0.4	0.3			
Cestrum guatemalensis Francey	Solanaceae	Early	15.3	5.2	2.1	1.8	1.1	1.5	0.3	0.9
Clethra suaveolens Turcz.	Clethraceae	Late							0.4	
Clethra macrophylla Martens & Gal.	Clethraceae	Late				0.2	0.5	1.9	1.2	0.9
Cleyera theaeoides (Sw.) Choisy	Theaceae	Mid				2.6	6.0	2.2	3.4	11.7
Cornus disciflora DC.	Cornaceae	Mid		2.4	3.4	3.0	2.1	1.4	5.7	1.5
Cornus excelsa Kunth	Cornaceae	Early					0.7			
Crataegus pubescens (H.B.K.) Steudel	Rosaceae	Early		1.8	2.1				0.3	
Cyathea fulva (Mart. & Gal.) Fée	Cyatheaceae	Early								1.3
Daphnopsis selerorum Gilg	Thymeliaceae	Late					0.5	0.4	0.3	0.9
Eupatorium karwinskianum DC.	Compositae	Mid							0.3	0.4
Eupatorium ligustrinum DC.	Compositae	Early		0.8	0.9	0.2				
Eupatorium macrophyllum L.	Compositae	Early	10.2			0.2				
Eupatorium mairetianum DC.	Compositae	Early		3.1				0.4		
Eupatorium nubigenum Benth.	Compositae	Late			0.7	0.4	1.2	1.3	1.4	1.1
Eupatorium sordidum Less.	Compositae	Early					0.5	1.1	0.6	0.3
Fuchsia encliandra Steudel	Onagraceae	Mid			0.5					
Fuchsia microphylla H.B.K.	Onagraceae	Mid		1.0	0.4	0.2	0.3		0.8	
Fuchsia splendens Zucc.	Onagraceae	Mid						0.3		0.4
Fuchsia thymifolia H.B.K.	Onagraceae	Mid		2.0	0.7	0.4	0.3	0.7	0.3	0.3

Table A.1.1 Continuation

Species	Family	Status	Grassland -10-20	Grassland -10-0	Forest 0-10	Forest 10-20	Forest 20-30	Forest 30-40	Forest 40-50	Forest 50-60
Garrya laurifolia Hartw. Ex Benth.	Garryaceae	Mid		1.6	1.9	0.5	1.2	0.5		0.3
Litsea glaucescens H.B.K.	Lauraceae	Mid		1.4	0.7			0.3	0.6	0.9
Magnolia sharpii Miranda	Magnoliaceae	Late			0.4	0.3	2.5	2.0	1.3	4.1
Miconia glaberrima (Schldl.) Naud.	Melastomataceae	Mid				0.6	1.4	0.5	0.6	10.8
Miconia oligotricha (DC.) Naudin	Melastomataceae	Mid					0.6			0.7
Monnina xalapensis H.B.K.	Polygalaceae	Early	23.9	4.0	0.5	0.3	0.3			
Myrica cerifera L.	Myricaceae	Early						0.4		
Olmediella betschleriana (Goeppert) Loes.	Flacourtiaceae	Late					0.3			
Oreopanax xalapensis (H.B.K.) Decne. & Planch.	Araliaceae	Mid		4.3	3.2	4.7	5.4	5.8	5.8	5.1
Parathesis leptopa Lundell	Mysinaceae	Mid					0.3	0.3		
Persea americana Miller	Lauraceae	Mid		1.0	3.5	1.3	7.0	9.7	6.2	5.4
Phoebe siltepecana aff. acuminatissima Lundell	Lauraceae	Mid				0.6	0.8	1.3		0.3
Pinus ayacahuite Ehrenb.	Pinaceae	Early		3.6		2.4			3.8	
Pinus montezumae Lamb.var. *montezumae*	Pinaceae	Early			5.4		1.8	4.3		
Pinus tecunumanii Martínez	Pinaceae	Early		15.5	10.5	17.5	1.0	9.3	23.1	
Pinus pseudostrobus Lindley var. *pseudostrobus*	Pinaceae	Early	13.3	1.9	2.9			1.2	0.7	8.7
Prunus rhamnoides Koehne	Rosaceae	Late		1.3	3.8	2.3	1.4	0.9	0.3	6.8
Prunus serotina Ehrh. ssp. *capuli* (Cav.) McVaugh	Rosaceae	Early		2.5	3.0	2.7	1.5		0.9	2.1
Quercus skutchii Trel.	Fagaceae	Mid					4.4			
Quercus benthamii A. DC.	Fagaceae	Mid				1.0	1.7			
Quercus crassifolia Humb. & Bonpl.	Fagaceae	Mid				4.1	4.4		7.4	3.6
Quercus laurina Humb. & Bonpl.	Fagaceae	Mid		8.5	14.9	22.0	20.9	21.8	11.1	9.5
Quercus rugosa Née	Fagaceae	Early			0.4	1.2	1.1	0.8		
Rapanea juergensenii Mez	Myrsinaceae	Mid		10.9	9.7	11.7	10.0	10.6	7.9	10.2

Table A.1.1 Continuation

Species	Family	Status	Grassland -10-20	Grassland -10-0	Forest 0-10	Forest 10-20	Forest 20-30	Forest 30-40	Forest 40-50	Forest 50-60
Rhamnus sharpii Johnston, M.	Rhamnaceae	Late		3.5	2.8	1.5	2.6	4.9	2.8	1.5
Saurauia latipetala Hemsley	Actinidiaceae	Mid				1.3	1.6	1.1		0.7
Senecio acutangulus (Bertol.) Hemsley	Compositae	Early						0.3		
Senecio barba-johannis DC.	Compositae	Mid					0.3	0.3		
Senecio cristobalensis Greenman ex Loes.	Compositae	Mid				1.2				
Solanum lanceolatum Berthault	Solanaceae	Early						0.3	0.3	
Solanum nigricans Martens & Gal.	Solanaceae	Early		0.7	1.2	0.6		0.3	0.9	0.8
Styrax argenteus Presl var. *ramirezii* (Greenm.) Gonsoulin	Styracaceae	Late					1.6	1.1	0.4	0.3
Symplocos limoncillo Humb. & Bonpl.	Symplocaceae	Mid			1.0	0.9	1.6	1.2	2.1	0.5
Synardisia venosa (Mast.) Lundell	Mircinaceae	Mid							0.3	0.9
Ternstroemia lineata DC.	Theaceae	Late			3.9	3.8	1.5	2.2	1.4	1.0
Ternstroemia pringlei (Rose) Standley	Theaceae	Late		1.3	3.6	2.1	2.0	3.2	1.1	3.6
Tournefortia densiflora Martens & Gal.	Boraginaceae	Mid				0.4	0.5			
Verbesina perymenioides Sch.-Bip. Ex Klatt	Compositae	Early		9.6	4.4	2.9	1.9	2.2	1.0	0.4
Viburnum biscolor Benth.	Caprifoliaceae	Early						0.3	0.3	
Viburnum jucundum Morton *ssp. jucundum*	Caprifoliaceae	Mid		3.9	3.9	1.6	2.8	1.2	2.4	0.6
Xylosma chiapensis Lundell	Flacourtiaceae	Mid								0.3
Zanthoxylum foliolosum Donn.-Sm.	Rutaceae	Mid		1.0	1.2	0.7	1.4	0.8	2.0	0.9
Zanthoxylum melanostictum Cham. & Schldl.	Rutaceae	Late							0.4	
Total RIV (%)				100	100	100	100	100	100	100

Table A.1.2 Relative importance values (RIV) for seedlings of each species along the grassland-edge-forest gradient (plots at different positions from the edge). Negative distances indicate metres into the grassland and positive number indicate metres into the forest from the edge. The importance values (%) were calculated for each species considering the number of stems, accumulated basal area and frequency in each plot along the grassland-edge-forest gradient.

			Grassland		Forest					
Species	**Family**	**Status**	**-10-20**	**-10-0**	**0-10**	**10-20**	**20-30**	**30-40**	**40-50**	**50-60**
Not identified							3.5			
Cestrum guatemalensis Francey	Solanaceae	Early	100.0	14.2	1.2	9.3	9.0	2.4		2.6
Cornus disciflora DC.	Cornaceae	Mid		5.8	0.7	6.9			4.8	5.1
Daphnopsis selerorum Gilg	Thymeliaceae	Late						2.5		
Eupatorium mairetianum DC.	Compositae	Early		5.6						
Eupatorium nubigenum Benth.	Compositae	Late					7.2	6.1		
Fuchsia microphylla H.B.K.	Onagraceae	Mid			0.4	3.4			4.8	
Fuchsia splendens Zucc.	Onagraceae	Mid					5.5	2.3		
Fuchsia thymifolia H.B.K.	Onagraceae	Mid			0.7	13.0		2.3		2.6
Garrya laurifolia Hartw. ex Benth.	Garryaceae	Mid		6.0						
Litsea glaucescens H.B.K.	Lauraceae	Mid							3.9	
Monnina xalapensis H.B.K.	Polygalaceae	Early		8.5	0.7				3.6	2.6
Oreopanax xalapensis (H.B.K.) Decne. & Planch.	Araliaceae	Mid		5.6	0.6	15.6	14.1	14.3	14.2	5.2
Phoebe siltepecana aff. *acuminatissima* Lundell	Lauraceae	Mid						3.5		
Pinus ayacahuite Ehrenb.	Pinaceae	Early								3.8
Prunus rhamnoides Koehne	Rosaceae	Late		5.8		4.7	3.5	5.8	7.6	
Prunus serotina Ehrh. ssp. *capuli* (Cav.) McVaugh	Rosaceae	Early		14.8	0.7	2.3			6.1	
Quercus laurina Humb. & Bonpl.	Fagaceae	Mid		5.6	1.1	10.5		9.2	6.0	13.0
Rapanea juergensenii Mez	Myrsinaceae	Mid		16.9	73.5	8.1	17.8	7.4	35.4	34.5
Rhamnus sharpii Johnston, M.	Rhamnaceae	Late		5.6	18.2	2.3	19.6	2.3		2.6

Table A.1.2 Continuation

Species	Family	Status	Grassland -10-20	Grassland -10-0	Forest 0-10	Forest 10-20	Forest 20-30	Forest 30-40	Forest 40-50	Forest 50-60
Senecio barba-johannis DC.	Compositae	Mid						4.8		
Senecio cristobalensis Greenman ex Loes.	Compositae	Mid					5.6	3.8		
Solanum nigricans Martens & Gal.	Solanaceae	Early					5.5	6.9		7.8
Styrax argenteus Presl var. *ramirezii* (Greenm.) Gonsoulin	Styracaceae	Late						5.4	2.5	
Symplocos limoncillo Humb. & Bonpl.	Symplocaceae	Mid						2.4	2.4	
Ternstroemia lineata DC.	Theaceae	Late				2.4			4.0	7.1
Ternstroemia pringlei (Rose) Standley	Theaceae	Late			0.9	2.5	5.2	2.4		3.9
Verbesina perymenioides Sch.-Bip. ex Klatt	Compositae	Early			1.4	16.7	3.5	5.8	2.4	4.1
Viburnum jucundum Morton ssp. *jucundum*	Caprifoliaceae	Mid		5.6		2.3		10.3		2.6
Zanthoxylum foliolosum J.D. Smith	Rutaceae	Mid							2.4	2.6
Total RIV (%)				100	100	100	100	100	100	100

Table A.1.3 ANOVA of the influence of distance from the edge into the forest (0-10, 10-20, 20-30, 30-40, 40-50 and 50-60 m) on the total basal area of large saplings.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	5	45.28	9.06	0.86	0.518
Site	5	58.45	11.70	1.12	0.377
Error	25	261.70	10.47		
Total	35	365.44			

Table A.1.4 ANOVA of the influence of distance from the edge into the forest (0-10, 10-20, 20-30, 30-40, 40-50 and 50-60 m) on the total basal area of trees.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	5	11225.6	2245.12	1.03	0.423
Site	5	39188.4	7837.68	3.59	0.014
Error	25	54632.2	2185.29		
Total	35	105046.2			

Table A.1.5 ANOVA of the influence of distance from the edge into the forest (0-10, 10-20, 20-30, 30-40, 40-50 and 50-60 m) on the total stem density of small saplings.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	5	0.283	0.057	0.75	0.591
Site	5	0.464	0.093	1.24	0.322
Error	25	1.877	0.075		
Total	35	2.624			

Table A.1.6 ANOVA of the influence of distance from the edge into the forest (0-10, 10-20, 20-30, 30-40, 40-50 and 50-60 m) on the total stem density of large saplings.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	5	0.304	0.061	1.07	0.399
Site	5	1.458	0.292	5.15	0.002
Error	25	1.415	0.057		
Total	35	3.176			

Table A.1.7 ANOVA of the influence of distance from the edge into the forest (0-10, 10-20, 20-30, 30-40, 40-50 and 50-60 m) on the total stem density of trees.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	5	0.054	0.011	0.40	0.841
Site	5	0.220	0.044	1.64	0.185
Error	25	0.669	0.027		
Total	35	0.944			

Table A.1.8 ANOVA of the influence of distance from the edge into the forest (0-10, 10-20, 20-30, 30-40, 40-50 and 50-60 m) on the total stem density of seedlings.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	5	1.067	0.213	0.90	0.496
Site	5	0.284	0.057	0.24	0.941
Error	25	5.924	0.237		
Total	35	7.276			

Table A.1.9 Results of regression analysis of the influence of canopy openness (estimated 1.5 m above the soil) on the total stem density of seedlings.

Source of variation	df	S.S.	M.S.	*F*	*P*
Regression	1	0.467	0.467	3.41	0.074
Error	34	4.660	0.137		
Total	35	5.126			

Table A.1.10 ANOVA of the influence of distance from the edge into the forest (0-10, 10-20, 20-30, 30-40, 40-50 and 50-60 m) on the canopy openness.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	5	0.122	0.024	1.22	0.329
Site	5	0.149	0.029	1.50	0.226
Error	25	0.498	0.020		
Total	35	0.769			

Table A.1.11 ANOVA of the influence of habitat (forest edge, 0-10 m and forest interior, 40-50 m) on the mean canopy height.

Source of variation	df	S.S.	M.S.	*F*	*P*
Habitat	1	4.18	4.18	0.13	0.729
Site	5	41.76	8.35	0.26	0.913
Error	5	155.86	31.17		
Total	11	201.81			

Table A.1.12 ANOVA of the influence of distance from the edge into the forest (0-10, 10-20, 20-30, 30-40, 40-50 and 50-60 m) on the species diversity index.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	5	0.273	0.055	1.20	0.339
Site	5	0.739	0.148	3.24	0.022
Error	25	1.141	0.046		
Total	35	2.154			

Table A.1.13 ANOVA of the influence of distance from the edge into the forest (0-10, 10-20, 20-30, 30-40, 40-50 and 50-60 m) on the evenness index.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	5	0.022	0.004	1.17	0.353
Site	5	0.014	0.003	0.73	0.606
Error	25	0.096	0.004		
Total	35	0.133			

Table A.1.14 ANOVA of the influence of distance from the edge into the grassland (0 to 10, 0 to -10 and –10 –20 m) on the total basal area of large saplings.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	2	58.77	29.39	1.56	0.256
Site	5	144.04	29.80	1.53	0.264
Error	10	187.74	18.77		
Total	17	503.59			

Table A.1.15 ANOVA of the influence of distance from the edge into the grassland (0 to 10, 0 to -10 and –10 –20 m) on the total stem density of seedlings.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	2	1.658	0.829	4.64	0.037
Site	5	1.819	0.364	2.04	0.158
Error	10	1.786	0.179		
Total	17	5.263			

Table A.1.16 ANOVA of the influence of distance from the edge into the grassland (0 to 10, 0 to -10 and –10 –20 m) on the total stem density of small saplings.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	2	0.578	0.289	5.95	0.020
Site	5	0.409	0.082	1.69	0.226
Error	10	0.486	0.049		
Total	17	1.474			

Table A.1.17 ANOVA of the influence of distance from the edge into the grassland (0 to 10, 0 to -10 and –10 –20 m) on the total stem density of large saplings.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	2	0.612	0.306	1.12	0.365
Site	5	0.126	0.025	0.09	0.992
Error	10	2.738	0.274		
Total	17	3.476			

Table A.1.18 Results of ANOVA on the influence of distance from the edge into the grassland (0 to 10, 0 to -10 and –10 –20 m) on the species diversity index.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	2	2.989	1.494	33.19	0.000
Site	5	0.663	0.133	2.95	0.069
Error	10	0.450	0.045		
Total	17	4.102			

Table A.1.19 ANOVA of the influence of distance from the edge into the grassland (0 to 10, 0 to -10 and –10 –20 m) on the evenness index.

Source of variation	df	S.S.	M.S.	*F*	*P*
Distance from the edge	2	1.426	0.713	25.26	0.000
Site	5	0.190	0.038	1.35	0.322
Error	10	0.282	0.028		
Total	17	1.898			

Table A.1.20 ANOVA of the influence of distance from the edge (-20, -10, 0, 10, 20, 30) and edge groups or types (Soft: PM, MD and NM and Hard: NP, PP and MP) on the vegetation cover estimated at the soil level.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.278	0.278	9.57	0.005
Distance from the edge	5	6.555	1.311	45.15	0.000
Edge type x Distance	5	0.656	0.131	4.52	0.005
Error	24	0.697	0.029		
Total	35	8.186			

Table A.1.21 ANOVA of the influence of distance from the edge (-20, -10, 0, 10, 20, 30) and edge groups or types (Soft: PM, MD and NM and Hard: NP, PP and MP) on the PAR measured at the soil level.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.182	0.182	0.58	0.454
Distance from the edge	5	16.671	3.334	10.60	0.000
Edge type x Distance	5	0.518	0.104	0.33	0.890
Error	24	7.547	0.314		
Total	35	24.918			

Appendix 2: Chapter 3

Table A.2.1 ANOVA of the influence of acorn treatment (metal tagged and untagged acorns) on the total acorn germination of *Q. laurina*.

Source of variation	df	S.S.	M.S.	*F*	*P*
Acorn treatment	1	0.025	0.025	0.16	0.729
Replicate	2	0.051	0.025	0.16	0.860
Error	2	0.311	0.155		
Total	5	0.386			

Table A.2.2 ANOVA of the influence of year (2000 and 2001), edge type (hard and soft), distance from the edge (0, 20, 40, and 60 m), and their interactions on the total acorn production.

Source of variation	df	S.S.	M.S.	*F*	*P*
Year	1	6.755	6.755	35.13	0.000
Edge type	1	0.019	0.019	0.10	0.752
Distance from the edge	3	0.348	0.116	0.60	0.618
Year x Edge type	1	0.223	0.223	1.16	0.291
Year x Distance	3	0.295	0.098	0.51	0.678
Edge type x Distance	3	0.208	0.069	0.36	0.782
Year x Edge type x Distance	3	0.175	0.058	0.30	0.823
Error	30	5.771	0.192		
Total	45	13.992			

Table A.2.3 ANOVA of the influence of year (2000 and 2001), edge type (hard and soft), distance from the edge (0, 20, 40, and 60 m), and their interactions on the proportion of germinated acorns.

Source of variation	df	S.S.	M.S.	*F*	*P*
Year	1	0.0018	0.0018	0.407	0.529
Edge type	1	0.0000	0.0000	0.004	0.948
Distance from the edge	3	0.0042	0.0014	0.327	0.806
Year x Edge type	1	0.0002	0.0002	0.041	0.840
Year x Distance	3	0.0013	0.0004	0.100	0.959
Edge type x Distance	3	0.0029	0.0010	0.220	0.882
Year x Edge type x Distance	3	0.0096	0.0032	0.739	0.537
Error	30	0.1300	0.0043		
Total	45	0.150			

Table A.2.4 ANOVA of the influence of year (2000 and 2001), edge type (hard and soft), distance from the edge (0, 20, 40, and 60 m), and their interactions on the proportion of acorns damaged by insects.

Source of variation	df	S.S.	M.S.	*F*	*P*
Year	1	0.0005	0.0005	0.01	0.906
Edge type	1	0.0014	0.0014	0.04	0.844
Distance from the edge	3	0.0926	0.0309	0.90	0.454
Year x Edge type	1	0.0056	0.0056	0.16	0.690
Year x Distance	3	0.0203	0.0068	0.20	0.898
Edge type x Distance	3	0.0374	0.0125	0.36	0.781
Year x Edge type x Distance	3	0.0390	0.0130	0.38	0.769
Error	30	1.0310	0.0344		
Total	45	1.2400			

Table A.2.5 ANOVA of the influence of year (2000 and 2001), edge type (hard and soft), distance from the edge (0, 20, 40, and 60 m), and their interactions on the proportion of acorns damaged by small mammals.

Source of variation	df	S.S.	M.S.	*F*	*P*
Year	1	0.00001	0.00001	0.00	0.985
Edge type	1	0.10200	0.10200	5.90	0.021
Distance from the edge	3	0.09387	0.03129	1.82	0.166
Year x Edge type	1	0.00403	0.00403	0.23	0.632
Year x Distance	3	0.06903	0.02301	1.33	0.281
Edge type x Distance	3	0.04464	0.01488	0.86	0.471
Year x Edge type x Distance	3	0.01981	0.00660	0.38	0.766
Error	30	0.51700	0.01723		
Total	45	0.84400			

Table A.2.6 Results of the regression analysis of the influence of trapping success of *Peromyscus* species on the total acorn removal of *Q. laurina*.

Source of variation	df	S.S.	M.S.	*F*	*P*
Regression	1	12883.90	12883.90	33.92	0.000
Error	34	12914.49	379.84		
Total	35	25798.39			

Edge effects on acorn removal: a pilot study

In order to explore differences in acorn removal due to distances from the forest edge and seed density, from the middle of July to August 2000, a study was carried out in three grasslands with a forest edge. The grasslands were temporarily ungrazed and surrounded by a Private Forest Reserve called "Moxviquil". Mature forest was vertically structured into two layers. The tallest trees form a canopy of 70-80 % of cover at a height of 25-30 m. Canopy dominants are *Q. segoviensis* and *Q. crassifolia*, and to lesser extent *Q. rugosa, Q. crispipilis* var. *panossifolia* and *P. tecunumanii.* Frequent species of near to edge plots were *Bacharis vaccinioides, Crataegus pubescens, Eupatorium ligustrinum, Monina xalapensis* and *Q. segoviensis.* The grassland of the site 1 has a few scattered shrubs of *Crataegus pubescens*. The low herb layer includes species such as: *Pennisetum clandestinum, Paspalum nigricans* and *Zeugites americana.*

Q. candicans acorns were collected from January to March 2000, at the Huitepec reserve, San Cristóbal de las Casas, Chiapas (2400 m). Two parallel transects (separated by 20 m) were established and groups of acorns were placed every eight metres at different distances from the edge into the forest and into the grassland (56, 48, 40, 32, 24, 16, 8, 0, -8, -16, -24, -32 m; negative symbol preceding the distance value refers to distance into the grassland). One transect had one acorn per point and the other piles of five acorns. Acorns removed were counted every third day during the first week and weekly thereafter. Additionally, the effect of grassland heterogeneity on acorn survival was tested at one site at Moxviquil. This site has a forest edge with two types of adjacent vegetation, one type has an advancing or soft edge with a dense shrub cover and the other one has an abrupt change in vegetation cover. Only 20 metres separate these two types of edges. Unfortunately at this site no other replicate was available, however, the site provided an opportunity to explore how acorn removal is variable spatially and to what extent the variability depends on vegetation structure. At the same time as the previous study, two parallels transects were positioned separated by 20 m, one under the soft edge and the other under the hard edge. Groups of acorns of *Q. candicans* (10 acorns each) were placed every

eight metres on both transects at different distances from the edge into the forest and into the grassland (56, 48, 40, 32, 24, 16, 8, 0, -8, -16, -24 and -32 m). Acorns removed were counted every third day during the first week and weekly thereafter.

Statistical analysis

Because of the homogeneity of acorn removal within habitats, values for each distance from the edge into the forest and into the grassland were pooled. Three habitats were defined: grassland (-40 to -16 m), edge (-8, 0 and 8 m) and forest interior (16 to 40 m). A categorical variable was created based in the binary response: removed or not removed when one acorn was placed, and at least one acorn removed when five acorns were placed. A categorical modelling approach CATMOD, a procedure of categorical data analogous to ANOVA, was used (SAS v. 8.0, SAS Institute Inc.). The model included the experimental factors: acorn density (one or five acorns) and habitat (forest, grassland and edge).

In a second analysis, temporal patterns of probability of detecting acorn piles over time were compared for the experimental factors: density and habitat using the Wilcoxon-Gehan test and the pairwise comparisons and test for heterogeneity among levels within the factors (Life tables procedure, SPSS v.10.0.1).

Results and discussion

After 24 days of exposure to predators, total acorn removal was only affected by habitat type (χ^2 =17.63, df=2, P<0.001, CATMOD). Acorn removal was higher in the edge and in the forest, however, decreased abruptly in the grasslands (Fig. A.2.1). This kind of response for acorn removal can be classified as a "Matrix effect" (Lidicker 1999) or a "Hard edge" (Duelli *et al.* 1990), where there is an abrupt change of any response variable crossing the edge due to different habitat types. Probability of detection through time was affected by habitat type (Wilcoxon-Gehan χ^2 =38.22, df=2, P<0.001) and by seed density (χ^2 =4.56, df=1, P=0.033). Piles of acorns (either with one or five acorns) were detected more rapidly in the forest edge

(-8, 0 and 8 m) compared with the grassland (-40 to -16 m) and the forest interior (16 to 40 m; Fig. A.2.2). This different edge response compared with the grassland and the forest interior is defined as an "Edge effect" (Lidicker 1999), where the edge has an emergent property and can be defined as a separate habitat.

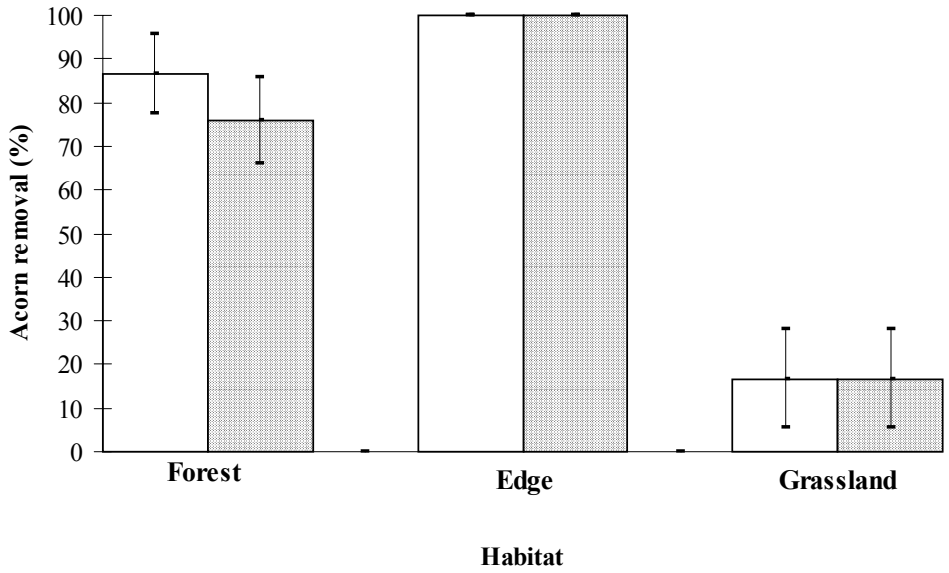

Fig. A.2.1 Mean acorn removal (± 1 SE) at the end of the experiment as a function of habitat type and seed density, five acorns (shaded bars) and one acorn (open bars).

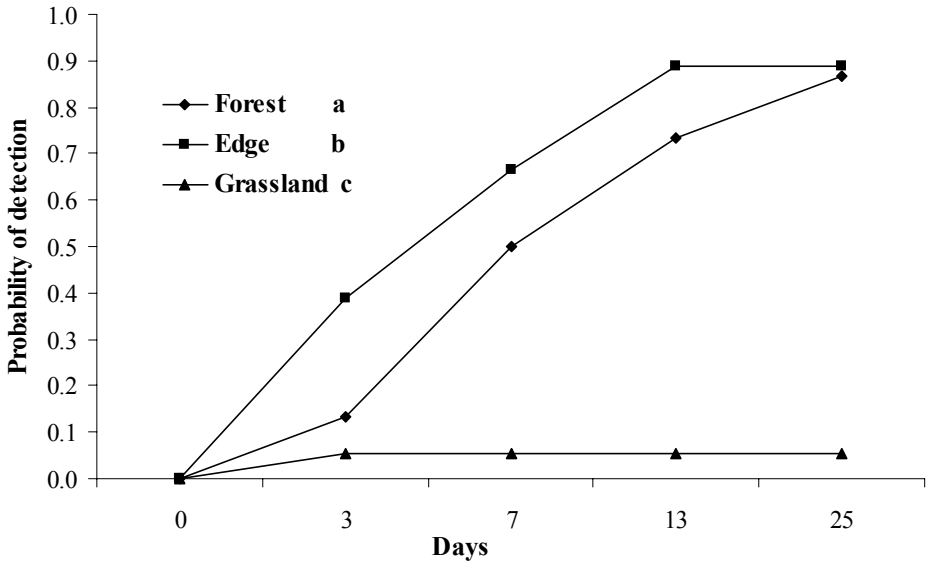

Fig. A.2.2. Probability of detection of a pile of *Q. candicans* acorns through time for each habitat type.

Piles of five acorns were detected and consumed more rapidly compared with single acorns (Fig. A.2.3).

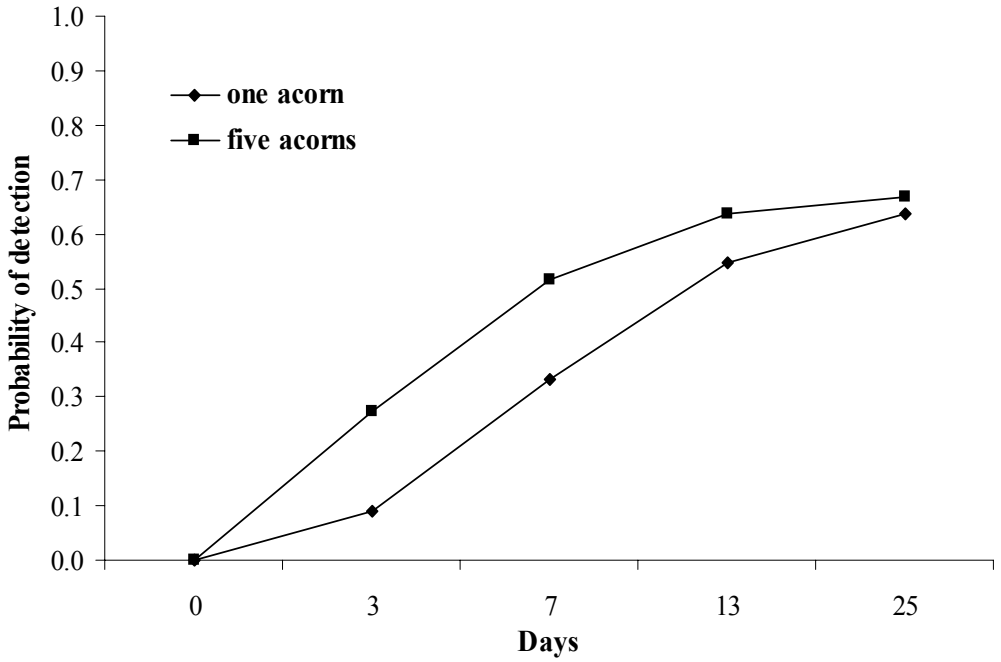

Fig. A.2.3 Probability of detection of a pile of *Q. candicans* acorns through the time for each seed density (one or five acorns).

Acorn removal was more intense under the soft edge and continued for 32 m into the grassland (Fig A.2.4). This suggests that seed predator's mobility from the forest into the grassland was higher across this edge type (edge permeability). The different responses in such a small spatial scale are also evidence of how the small mammals respond to microenvironments within a habitat type. Although grasslands are the habitat of some small mammal species as *Sigomodon hispidus* (small-seed eater), the lower acorn removal in the grasslands make me think that the small mammals that remove the acorns under the advancing edge live within the forest (as *Peromyscus* spp.) and penetrate into the open site. Because of the lack of replicates and small mammal trapping it is difficult to generalise the process and analyse it statistically. Basically, this pilot study suggested that acorn removal might be highly variable at small spatial scales, and that soft edges would have more edge permeability to small mammals (acorn predators/dispersers) in comparison to hard edges.

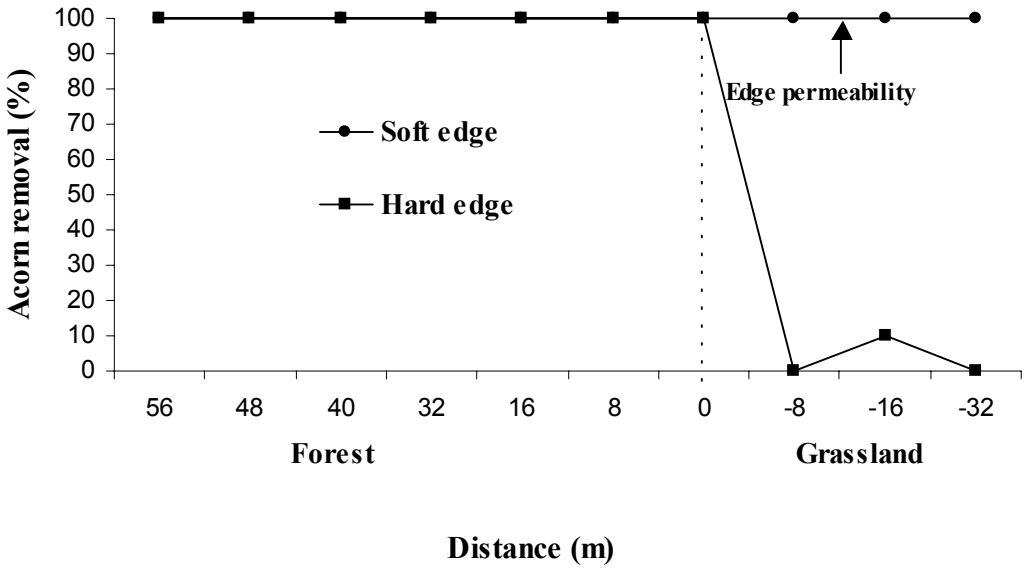

Fig. A.2.4 Acorn removal after 24 days along the forest-edge-grassland gradients in two transects placed in two different edge types (hard and soft edges separated by 20 m in the same site).

Appendix 3: Chapter 4

Table A.3 List of tree species and their DBH (diameter at breast height; cm) used as supports for the dishes in the experiment of acorn removal. Dishes were individually numbered. D.E. = distance from the edge (m).

NP: HARD EDGE				PP: HARD EDGE			
Dish	**DE**	**Species**	**DBH**	**Dish**	**DE**	**Species**	**DBH**
1	0	*Quercus crassifolia*	56	**1**	0	*Persea americana*	29.9
2	15	*Quercus crassifolia*	56	**2**	15	*Pinus tecunumanii*	32.5
3	30	*Quercus laurina*	40.5	**3**	30	*Quercus laurina*	32.5
4	45	*Persea americana*	31.4	**4**	45	*Persea americana*	32.6
5	60	*Cleyera theaeoides*	30.5	**5**	60	*Quercus laurina*	37
6	0	*Pinus pseudostrobus*	45.5	**6**	0	*Pinus tecunumanii*	33.2
7	15	*Prunus serotina*	32.8	**7**	15	*Persea americana*	30.5
8	30	*Stirax argenteus*	29.7	**8**	30	*Quercus crassifolia*	33
9	45	*Cleyera theaeoides*	31.3	**9**	45	*Quercus laurina*	54.5
10	60	*Quercus laurina*	37	**10**	60	*Cleyera theaeoides*	32.5/10
11	0	*Quercus laurina*	37	**11**	0	*Pinus tecunumanii*	33
12	15	*Magnolia sharpii*	29.8	**12**	15	*Quercus laurina*	31.5
13	30	*Quercus crassifolia*	57.5	**13**	30	*Quercus laurina*	30
14	45	*Quercus laurina*	32	**14**	45	*Quercus laurina*	53
15	60	*Quercus laurina*	63	**15**	60	*Persea americana*	29.5

MP: HARD EDGE				NM: SOFT EDGE			
Dish	**DE**	**Species**	**DBH**	**Dish**	**DE**	**Species**	**DBH**
1	0	*Quercus laurina*	43	**1**	0	*Pinus tecunumanii*	41
2	15	*Quercus laurina*	39	**2**	15	*Persea americana*	31.7
3	30	*Quercus laurina*	31	**3**	30	*Ternstroemia linneata*	34
4	45	*Quercus laurina*	36/30	**4**	45	*Pinus pseudostrobus*	30
5	60	*Rapanea juerguensenii*	29.9	**5**	60	*Prunus rhamnoides*	29.7
6	0	*Quercus crassifolia*	46.5	**6**	0	*Pinus pseudostrobus*	29.8
7	15	*Quercus laurina*	34.5	**7**	15	*Pinus tecunumanii*	48
8	30	*Quercus laurina*	32	**8**	30	*Pinus tecunumanii*	33
9	45	*Quercus laurina*	33.5	**9**	45	*Pinus pseudostrobus*	44
10	60	*Quercus laurina*	31	**10**	60	*Pinus pseudostrobus*	36.5
11	0	*Pinus pseudostrobus*	29.7	**11**	0	*Viburnum jucundum*	29.8
12	15	*Quercus laurina*	29.5	**12**	15	*Cleyera theaeoides*	29
13	30	*Quercus laurina*	37	**13**	30	*Quercus laurina*	87.5
14	45	*Quercus laurina*	37.5	**14**	45	*Pinus pseudostrobus*	31.9
15	60	*Quercus crassifolia*	34	**15**	60	*Pinus tecunumanii*	32

Table A.3 Continuation

PM: SOFT EDGE				MD: SOFT EDGE			
Dish	**DE**	**Species**	**DBH**	**Dish**	**DE**	**Species**	**DBH**
1	0	*Pinus tecunumanii*	36.5	**1**	0	*Quercus laurina*	35/23
2	15	*Rapanea juerguensenii*	31.9	**2**	15	*Pinus tecunumanii*	34.5
3	30	*Quercus laurina*	24.5	**3**	30	*Quercus laurina*	29.8
4	45	*Quercus laurina*	33	**4**	45	*Rhamnus sharpii*	31
5	60	*Quercus laurina*	33	**5**	60	*Pinus pseudostrobus*	32.5
6	0	*Rapanea juerguensenii*	31.5	**6**	0	*Quercus laurina*	31
7	15	*Pinus tecunumanii*	86	**7**	15	*Pinus tecunumanii*	33
8	30	*Quercus laurina*	36/21	**8**	30	*Quercus laurina*	76/32.5
9	45	*Quercus laurina*	31.7/32	**9**	45	*Quercus crassifolia*	43.5
10	60	*Quercus laurina*	49	**10**	60	*Rhamnus sharpii*	30
11	0	*Rapanea juerguensenii*	31.5	**11**	0	*Quercus laurina*	29.8
12	15	*Persea americana*	24.5/29.5	**12**	15	*Quercus crassifolia*	55
13	30	*Quercus laurina*	29.5/16.5	**13**	30	*Cornus disciflora*	30.2
14	45	*Quercus laurina*	29.5	**14**	45	*Cleyera theaeoides*	31.7
15	60	*Pinus pseudostrobus*	68	**15**	60	*Quercus crassifolia*	70

Appendix 4: Chapter 5

Table A.4.1 ANOVA of the influence of acorn species (*Q. laurina, Q. rugosa, Q. crassifolia* and *Q. candicans*) on the total germination at the end of the experiment.

Source of variation	df	S.S.	M.S.	*F*	*P*
Species	3	0.831	0.277	40.17	0.000
Replicate	4	0.027	0.007	00.99	0.455
Error	12	0.083	0.007		
Total	19	0.941			

Table A.4.2 ANOVA of the influence of edge type (hard and soft) and habitat (grassland, edge and forest) and their interaction on the soil moisture during April 2001.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.0001	0.0001	0.05	0.836
Habitat	2	0.0005	0.0003	0.17	0.845
Edge type x Habitat	2	0.0032	0.0016	1.03	0.388
Error	12	0.0183	0.0053		
Total	17	0.0221			

Table A.4.3 ANOVA of the influence of edge type (hard and soft) and habitat (grassland, edge and forest) and their interaction on the soil moisture during May 2001.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.0015	0.0015	3.28	0.095
Habitat	2	0.0016	0.0008	1.77	0.212
Edge type x Habitat	2	0.0007	0.0004	0.75	0.493
Error	12	0.0054	0.0005		
Total	17	0.0091			

Table A.4.4 ANOVA of the influence of edge type (hard and soft) and habitat (grassland, edge and forest) and their interaction on the soil moisture during June 2001.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.0010	0.0010	2.43	0.145
Habitat	2	0.0004	0.0002	0.48	0.630
Edge type x Habitat	2	0.0030	0.0015	3.67	0.057
Error	12	0.0050	0.0004		
Total	17	0.0095			

Table A.4.5 ANOVA of the influence of edge type (hard and soft) and habitat (grassland, edge and forest) and their interaction on the PAR reaching the soil surface.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.015	0.015	0.26	0.620
Habitat	2	8.598	4.299	72.82	0.000
Edge type x Habitat	2	0.045	0.023	0.38	0.691
Error	12	0.708	0.059		
Total	17	9.367			

Table A.4.6 MANOVA of the influence of edge type (hard and soft) and habitat (grassland, edge and forest) and their interaction on the final fate of the acorns (proportion germinating, germinating with insect damage, plumules, seedlings, viable, non-germinating rotten and with insect damage).

Source of variation	Pillai's Trace	df treatment	df error	*F*	*P*
Edge type	0.152	7	66	1.69	0.126
Habitat	0.544	14	134	3.58	0.000
Cover	0.355	7	66	5.18	0.000
Species	0.996	14	134	9.50	0.000
Edge type x Habitat	0.408	14	134	2.45	0.004
Edge type x Cover	0.074	7	66	0.76	0.624
Edge type x Species	0.167	14	134	0.87	0.589
Habitat x Cover	0.276	14	134	1.53	0.109
Habitat x Species	0.501	28	276	1.41	0.087
Cover x Species	0.208	14	134	1.11	0.353
Edge type x Habitat x Cover	0.314	14	134	1.78	0.048
Edge type x Habitat x Species	0.443	28	273	1.23	0.205
Edge type x Cover x Species	0.209	14	134	1.11	0.351
Habitat x Cover x Species	0.624	28	276	1.82	0.008
Edge type x Habitat x Cover x Species	0.423	28	276	1.16	0.264
Error					

Table A.4.7 ANOVA of the influence of experimental factors: T: Edge Type (hard and soft), H: Habitat (grassland, edge and forest), S: Species (*Q. crassifolia, Q. laurina, Q. rugosa*) and their interactions on the final acorn fates at the end of the study period (73 days). * = ($P \leq 0.05$), ** = ($P \leq 0.01$), *** = ($P \leq 0.001$), ns = ($P > 0.05$).

		Germinated								Non-germinated					
Source of Variation		**Radicle**		**Insect Damaged**		**Plumules**		**Seedlings**		**Rotten**		**Viable**		**Insect damaged**	
	df	S.S.	*F*	S.S.	*F*	S.S.	*F*	S.S.	*F*	S.S.	*F*	S.S.	*F*	S.S.	*F*
T	1	0.434	7.28**	0.311	5.10*	0.0000	0.001ns	0.051	1.10ns	0.003	0.08ns	0.027	0.71ns	0.021	0.45ns
H	2	0.488	4.09*	1.134	8.82**	0.072	1.22ns	1.381	14.85***	0.445	5.99**	0.217	2.80ns	0.393	4.18*
S	2	0.118	0.99ns	0.120	0.93ns	0.670	11.31***	3.458	37.18***	5.787	77.94***	0.712	9.20***	0.132	1.41ns
C	1	0.229	3.85ns	0.005	0.07ns	0.144	4.85*	0.154	3.30ns	0.263	7.07*	0.488	12.60***	0.079	1.67ns
TxH	2	0.190	1.59ns	0.049	0.38ns	0.010	0.17ns	0.382	4.10*	0.406	5.47*	0.159	2.05ns	0.124	1.32ns
TxS	2	0.042	0.35ns	0.146	1.14ns	0.023	0.38ns	0.089	0.96ns	0.032	0.43ns	0.088	1.14ns	0.147	1.57ns
TxC	1	0.090	1.51ns	0.006	0.09ns	0.007	0.24ns	0.013	0.28ns	0.008	0.22ns	0.053	1.36ns	0.003	0.04ns
HxS	4	0.647	2.72*	0.053	0.21ns	0.209	1.76ns	0.150	0.81ns	0.509	3.43*	0.079	0.51ns	0.438	2.33ns
HxC	2	0.126	1.06ns	0.195	1.51ns	0.015	0.25ns	0.559	6.01**	0.100	1.34ns	0.074	0.96ns	0.068	0.73ns
CxS	2	0.212	1.78ns	0.064	0.49ns	0.002	0.03ns	0.099	1.07ns	0.064	0.87ns	0.124	1.61ns	0.146	1.55ns
TxHxS	4	0.529	2.22ns	0.033	0.13ns	0.197	1.66ns	0.352	1.89ns	0.162	1.09ns	0.278	1.79ns	0.236	1.26ns
TxHxC	2	0.141	1.18ns	0.091	0.71ns	0.120	2.03ns	0.114	1.23ns	0.090	1.21ns	0.024	0.31ns	0.239	0.09ns
TxCxS	2	0.426	3.58*	0.029	0.23ns	0.016	0.27ns	0.013	0.14ns	0.079	1.07ns	0.017	0.22ns	0.257	2.73ns
HxSxC	4	0.121	0.51ns	0.111	0.43ns	0.661	5.58***	0.182	0.98ns	0.507	3.42*	0.046	0.30ns	0.201	1.07ns
TxHxSxC	4	0.120	0.50ns	0.307	1.19ns	0.146	1.23ns	0.185	0.99ns	0.127	0.85ns	0.201	1.30ns	0.101	0.54ns
Error	72	4.286		4.626		2.132		3.348		2.673		2.785		3.385	

Appendix 5: Chapter 6

Table A.5.1 Total seedling survivorship (TSS, %), maximum height of seedlings (MXH, cm), basal area (BA, mm^2), number of leaves (NL), and the relative index of leaf damage (RLD, % relative to the highest value recorded) for each species as a function of edge type and distance from the edge. Means are the average for each distance from the edge (transect) per species (n=150). Reported values are means (± 1 SE) at the end of the experiment (from July 2001 to May 2002).

Quercus candicans

Edge Type	Distance (m)	TSS	MXH	BA	NL	RLD
Hard	**-24**	67.4±17.2	18.5±0.6	15.9±2.8	6.0±1.6	62.2±4.4
	-12	77.8±6.4	16.4±1.1	13.0±1.6	7.5±0.5	66.7±0.0
	0	100.0±0.0	16.5±0.6	8.8±1.1	7.3±0.7	67.4±4.2
	12	84.3±4.6	14.0±0.3	7.7±0.8	4.0±0.4	69.8±2.3
	24	74.1±3.7	12.9±0.6	5.4±0.7	2.6±0.5	71.3±2.0
Soft	**-24**	96.3±3.7	16.3±0.4	18.7±6.5	6.1±0.6	61.1±7.8
	-12	100.0±0.0	19.9±2.1	16.3±2.7	8.4±0.9	57.0±4.0
	0	85.2±14.8	17.1±1.4	8.0±1.9	5.2±0.5	69.6±5.3
	12	93.0±3.5	15.6±1.1	5.7±0.6	5.0±1.0	75.2±4.6
	24	88.4±0.5	15.3±1.7	7.3±0.6	4.2±1.0	71.1±5.9

Quercus crassifolia

Edge type	Distance (m)	TSS	MXH	BA	NL	RLD
Hard	**-24**	76.7±18.6	18.5±0.6	25.2±8.0	15.5±5.1	45.2±3.2
	-12	80.5±15.5	16.4±1.1	26.6±8.1	13.1±4.5	48.3±4.2
	0	76.7±8.8	16.5±0.6	12.8±1.2	5.1±0.4	75.8±4.9
	12	56.4±1.8	14.0±0.3	8.1±0.7	3.2±0.9	73.0±12.6
	24	45.9±19.7	12.9±0.6	6.5±1.7	2.8±0.4	79.2±7.1
Soft	**-24**	100.0±0.0	16.3±0.4	17.5±1.8	11.8±1.8	46.9±3.5
	-12	100.0±0.0	19.9±2.1	18.9±1.9	8.8±2.3	52.9±7.6
	0	60.0±5.8	17.1±1.4	6.9±1.5	3.2±0.4	73.3±6.7
	12	30.0±25.2	15.6±1.1	5.9±1.5	3.9±1.6	66.7±0.0
	24	62.1±10.8	15.3±1.7	8.9±2.6	2.1±0.4	75.5±4.4

Table A.5.1 Continued.

Quercus laurina

Edge type	Distance (m)	TSS	MXH	BA	NL	RLD
Hard	**-24**	70.0±5.8	15.4±1.3	18.1±7.7	50.7±25.1	35.7±4.7
	-12	80.0±15.4	17.1±1.3	20.2±4.8	60.7±14.7	38.4±3.0
	0	96.7±3.3	15.9±0.2	11.7±2.3	20.0±1.6	56.9±5.8
	12	90.0±10.0	14.5±0.9	5.9±0.4	10.5±2.5	60.9±5.9
	24	96.7±3.3	15.6±1.0	7.4±0.6	13.6±2.4	59.6±3.3
Soft	**-24**	100.0±0.0	20.5±1.4	16.0±0.5	37.5±1.3	45.6±2.2
	-12	96.7±3.3	23.5±2.4	21.6±6.5	38.7±6.9	39.0±1.0
	0	79.6±9.8	16.1±1.7	9.5±2.1	15.6±0.5	58.9±2.3
	12	96.7±3.3	16.6±1.0	7.3±1.1	12.8±1.5	55.6±4.5
	24	86.7±13.3	15.3±0.5	6.7±1.0	11.3±0.4	58.6±1.8

Quercus rugosa

Edge type	Distance (m)	TSS	MXH	BA	NL	RLD
Hard	**-24**	76.7±18.6	13.2±0.5	18.4±3.4	12.1±2.9	57.1±1.9
	-12	96.3±3.7	14.6±0.8	30.0±15.0	19.2±4.4	47.2±6.0
	0	93.3±6.7	14.0±0.8	8.4±1.3	7.3±0.5	65.5±2.0
	12	93.6±3.2	14.9±0.3	6.8±0.6	5.6±0.1	70.6±5.8
	24	93.3±3.3	15.4±0.7	6.6±0.5	6.6±0.4	71.3±1.5
Soft	**-24**	100.0±0.0	17.4±1.2	16.9±1.9	11.5±0.8	68.1±4.5
	-12	96.7±3.3	18.7±1.0	14.6±1.6	11.2±0.5	57.1±11.1
	0	86.7±8.8	14.8±1.5	12.8±5.4	6.2±0.8	74.3±1.6
	12	93.3±3.3	15.5±0.2	7.0±1.1	6.8±0.6	67.3±5.2
	24	90.3±5.8	15.9±0.4	7.8±0.7	6.3±0.7	72.6±1.6

Quercus segoviensis

Edge type	Distance (m)	TSS	MXH	BA	NL	RLD
Hard	**-24**	86.7±13.3	14.2±0.4	14.6±1.5	9.3±3.3	53.0±2.2
	-12	84.8±15.1	13.5±0.9	13.7±4.5	8.1±2.9	62.8±7.5
	0	93.3±3.3	18.0±0.9	11.5±1.9	6.1±0.4	70.0±5.1
	12	86.3±8.7	15.5±2.8	6.9±1.1	3.2±0.7	80.4±5.2
	24	83.9±3.1	15.2±0.4	6.5±1.7	3.6±0.3	73.3±5.8
Soft	**-24**	100.0±0.0	17.9±0.7	10.7±1.2	9.5±0.7	66.7±8.9
	-12	100.0±0.0	19.7±0.8	13.0±3.2	8.4±1.0	58.6±4.1
	0	93.9±3.2	15.6±0.9	9.5±2.3	4.0±0.5	71.3±8.3
	12	96.7±3.3	17.0±1.3	8.2±2.1	4.0±0.8	78.5±11.4
	24	93.3±6.7	16.3±1.8	7.5±2.4	3.6±0.1	71.1±6.8

Table A.5.2 ANOVA of the influence of experimental factors: edge type (hard and soft), distance from the edge (-24, -12, 0, 12, 24 m), species (*Q. laurina, Q. rugosa* and *Q. crassifolia*) and their interactions on the difference in the leaf damage index during the study period.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.077	0.077	2.57	0.112
Distance	4	1.047	0.262	8.76	0.000
Species	4	0.795	0.199	6.65	0.000
Edge type x Distance	4	0.049	0.012	0.41	0.799
Edge type x Species	4	0.121	0.030	1.01	0.404
Distance x Species	16	0.298	0.019	0.62	0.857
Edge type x Distance x Species	16	0.266	0.016	0.56	0.909
Error	100	2.986	0.030		
Total	149	5.639			

Table A.5.3 ANOVA of the influence of experimental factors: edge type (hard and soft), distance from the edge (-24, -12, 0, 12, 24 m), date of sampling and their interactions on the mean soil moisture.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.00009	0.00009	0.03	0.866
Distance	4	0.00001	0.00280	0.83	0.506
Date	5	4.469	0.894	265.96	0.000
Edge type x Distance	4	0.00263	0.00059	0.18	0.950
Edge type x Date	5	0.01432	0.00286	0.85	0.516
Distance x Date	20	0.05243	0.00262	0.78	0.733
Edge type x Distance x Date	20	0.03450	0.00172	0.51	0.957
Error	120	0.403	0.00336		
Total	179	4.987			

Table A.5.4 ANOVA of the influence of experimental factors: edge type (hard and soft), distance from the edge (-24, -12, 0, 12, 24 m), date of sampling and their interactions on the mean PAR reaching the soil surface.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	2.623	2.623	26.54	0.000
Distance	4	62.272	15.668	158.51	0.000
Date	5	36.938	7.388	74.74	0.000
Edge type x Distance	4	0.973	0.243	2.46	0.049
Edge type x Date	5	1.018	0.204	2.06	0.075
Distance x Date	20	5.149	0.257	2.60	0.001
Edge type x Distance x Date	20	1.428	0.071	0.72	0.797
Error	120	11.861	0.098		
Total	179	122.661			

Table A.5.5 ANOVA of the influence of experimental factors: edge type (hard and soft), distance from the edge (-24, -12, 0, 12, 24 and their interaction on the total ground vegetation cover.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.0036	0.0036	0.88	0.360
Distance	4	0.414	0.104	25.17	0.000
Edge type x Distance	4	0.1798	0.0049	1.09	0.387
Error	20	0.0823	0.0041		
Total	29	0.518			

Table A.5.6 ANOVA of the influence of experimental factors: edge type (hard and soft), distance from the edge (-24, -12, 0, 12, 24 and their interaction on the species diversity index of the herbaceous and shrubs strata.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.0095	0.0095	1.97	0.175
Distance	4	0.0406	0.0101	2.11	0.117
Edge type x Distance	4	0.0070	0.0017	0.37	0.830
Error	20	0.0963	0.0048		
Total	29	0.154			

Table A.5.7 ANOVA of the influence of experimental factors: edge type (hard and soft), distance from the edge (-24, -12, 0, 12, 24 and their interaction on the species evenness index of the herbaceous and shrubs strata.

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.0146	0.0146	2.10	0.162
Distance	4	0.0833	0.0208	2.99	0.043
Edge type x Distance	4	0.0161	0.0029	0.42	0.794
Error	20	0.139	0.0069		
Total	29	0.249			

Table A.5.8 ANOVA of the influence of experimental factors: edge type (hard and soft), distance from the edge (-24, -12, 0, 12, 24 and their interaction on the maximum height of herbaceous strata (<50 cm)

Source of variation	df	S.S.	M.S.	*F*	*P*
Edge type	1	0.242	0.242	17.31	0.000
Distance	4	0.113	0.028	2.01	0.131
Edge type x Distance	4	0.276	0.069	4.93	0.006
Error	20	0.280	0.014		
Total	29	0.911			